

**A REVISION OF *PHYSOTARSUS* TOWNES, WITH A PRELIMINARY  
PHYLOGENETIC ANALYSIS OF SCOLOBATINI (HYMENOPTERA:  
ICHNEUMONIDAE: CTENOPELMATINAE)**

A Thesis

by

KIRA ZHAUROVA

Submitted to the Office of Graduate Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2006

Major Subject: Entomology

**A REVISION OF *PHYSOTARSUS* TOWNES, WITH A PRELIMINARY  
PHYLOGENETIC ANALYSIS OF SCOLOBATINI (HYMENOPTERA:  
ICHNEUMONIDAE: CTENOPELMATINAE)**

A Thesis

by

KIRA ZHAUROVA

Submitted to the Office of Graduate Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Approved by:

Chair of Committee,  
Committee Members,  
Head of Department,

Robert Wharton  
James Woolley  
Kirk Winemiller  
Kevin Heinz

August 2006

Major Subject: Entomology



## ABSTRACT

A Revision of *Physotarsus* Townes, with a Preliminary Phylogenetic Analysis of Scolobatini (Hymenoptera: Ichneumonidae: Ctenopelmatinae). (August 2006)

Kira Zhaurova, B.A., George Mason University

Chair of Advisory Committee: Dr. Robert Wharton

A species-level revision and a phylogenetic analysis of the genus *Physotarsus* Townes are performed. *Physotarsus* is expanded to include 17 new species: *P. albus* sp. nov., *P. claviger* sp. nov., *P. concavus* sp. nov., *P. cordatus* sp. nov., *P. emarginatus* sp. nov., *P. flavipennis* sp. nov., *P. foveatus* sp. nov., *P. gineus* sp. nov., *P. glabellus* sp. nov., *P. laucos* sp. nov., *P. luteus* sp. nov., *P. melipennis* sp. nov., *P. melotarsus* sp. nov., *P. niveus* sp. nov., *P. oculatus* sp. nov., *P. tonicus* sp. nov., and *P. truncatus* sp. nov. *Physotarsus fabioi* Gauld is removed from *Physotarsus* and the Scolobatini, and placed in Pionini (Ctenopelmatinae).

A phylogenetic analysis of the tribe Scolobatini yields two monophyletic groups of genera, reclassified as Scolobatini and Westwoodiini. Scolobatini includes the genera *Catucaba*, *Onarion*, *Physotarsus* and *Scolobates*, and Westwoodiini includes genera *Dictyopheltes*, *Hypopheltes*, *Pergaphaga* and *Westwoodia*. The genus *Tasmabates*, previously included in the Scolobatini, is excluded from both the Scolobatini and the Westwoodiini, its current placement unclear.

## ACKNOWLEDGEMENTS

I would like to express my gratitude to the people who aided me in my journey to this academic achievement. To Dr. Robert Wharton – for his guidance, counsel, and much, much more. To Dr. Jim Woolley – for his professional and academic advice, and moral support. To Dr. David Furth – for first introducing me to entomology, thus paving the grounds for my current accomplishments. To Dr. Ian Gauld and Dr. David Wahl – for sharing their immeasurable knowledge and experience in “ichneumonology”, and their memorable hospitality. To Dr. Ralph Eckerlin for fostering my general interest in biology and natural history. To Matthew J. Yoder – for his wide-reaching expertise and his infinite patience.

I would also like to thank the institutions, such as the American Entomological Institute, which had loaned me material used in this work. Additionally, I’d like to thank the TAMU Department of Entomology faculty and staff for their academic and administrative expertise. Finally, I want to thank my friends and family for support and encouragement.

## TABLE OF CONTENTS

|  | Page |
|--|------|
| ABSTRACT .....   | iii  |
| ACKNOWLEDGEMENTS.....                                      | iv   |
| TABLE OF CONTENTS .....                                    | v    |
| LIST OF TABLES .....                                       | vii  |
| CHAPTER  |      |
| I     INTRODUCTION .....                                   | 1    |
| II    MATERIALS AND METHODS .....                          | 3    |
| Materials .....  | 3    |
| Data acquisition and specimen examination .....            | 3    |
| Description – format and terminology .....                 | 4    |
| Phylogenetic analyses .....                                | 10   |
| III   REVISION OF <i>PHYSOTARSUS</i> TOWNES, 1966.....     | 12   |
| Overview of <i>Physotarsus</i> Townes, 1966 .....          | 12   |
| <i>Physotarsus</i> Townes, 1966: key to species .....      | 14   |
| <i>Physotarsus</i> Townes, 1966: species descriptions..... | 17   |
| IV    GENERIC REVISION OF SCOLOBATINI .....                | 59   |
| Overview of Scolobatini .....                              | 59   |
| Discussion of the revised Scolobatini classification ..... | 60   |
| Generic revision of the Scolobatini .....                  | 64   |
| Scolobatini taxa .....                                     | 65   |
| Generic revision of the Westwoodiini .....                 | 73   |
| Westwoodiini taxa .....                                    | 75   |
| V     PHYLOGENETIC ANALYSIS OF <i>PHYSOTARSUS</i>          |      |
| TOWNES, 1966.....  | 81   |
| Included taxa .....  | 81   |
| Characters.....  | 82   |
| Analyses: results and discussion .....                     | 93   |
| VI    PHYLOGENETIC ANALYSES OF SCOLOBATINI .....           | 97   |
| Included taxa .....  | 97   |
| Characters.....  | 98   |
| Analyses: results and discussion .....                     | 110  |
| VII   CONCLUSION .....                                     | 114  |
| REFERENCES .....   | 115  |

|                                    | Page |
|------------------------------------|------|
| APPENDIX A FIGURES AND TABLES..... | 120  |
| VITA.....                          | 155  |

## LIST OF TABLES

| TABLE   | Page |
|---|------|
| 1. Checklist of the <i>Physotarsus</i> species .....                                | 14   |
| 2. Matrix 1 Phylogenetic analysis of <i>Physotarsus</i> .....                       | 149  |
| 3. Tree 1 Phylogenetic analyses of <i>Physotarsus</i> .....                         | 150  |
| 4. Tree 2 Phylogenetic analyses of <i>Physotarsus</i> .....                         | 151  |
| 5. Tree 3 Phylogenetic analyses of <i>Physotarsus</i> : strict consensus tree ..... | 152  |
| 6. Matrix 2 Phylogenetic analyses of Scolobatini .....                              | 153  |
| 7. Phylogenetic analyses of Scolobatini: consensus topology .....                   | 154  |

## CHAPTER I

### INTRODUCTION

The family Ichneumonidae (Hymenoptera: Ichneumonoidea) is the most speciose hymenopteran group, currently containing over 21,805 valid species (Yu and Horstmann 1997), with some species estimates reaching as high as 100,000 species worldwide (Gauld 1997). Most of the current classification was established by Henry Townes, who delineated a total of 25 subfamilies in his “Genera of Ichneumonidae I-IV” (Townes 1969, 1970 a, b, 1971). The most recent treatment recognized 37 subfamilies (Gauld and Wahl 2002), while the latest estimate of the total number of valid Ichneumonid genera, 1485, was given by Yu and Horstmann (1997). The subfamily Ctenopelmatinae (=Scolobatinae *sensu* Townes and Townes, 1959) is a moderately large and morphologically diverse ichneumonid subfamily with over 100 currently valid genera and over 1100 described species (Yu and Horstmann 1997). The ctenopelmatine tribe Scolobatini is distributed world-wide (except Africa), and is theorized to contain the most basal ctenopelmatines (Gauld, personal communication). The most detailed and recent works on Scolobatini are those of Ian Gauld (1984, 1997). No cladistic analyses are available for the Scolobatini, nor for the subfamily Ctenopelmatinae as a whole.

Scolobatines are koinobiont endoparasitoids of sawflies in the families Pergidae and Argidae (Gauld 1984, Gauld 1997). They range in body length from 3mm to over 2.5cm for some of the largest Australian species. Current records indicate highest species richness in Australia and Central America, but notably those are the only regions studied in detail. Very few host records are available overall, especially for the New World Scolobatini.

The tribe Scolobatini was first described/recognized by Schmiedeknecht (1911). The tribe is currently composed of three New World genera, *Physotarsus* Townes, 1966, *Onarion* Townes, 1970b and *Catucaba* Graf, Kumagai, Dutra, 1991, one Holarctic genus, *Scolobates* Gravenhorst, 1829, and five Australian genera, *Dictyopheltes* Gauld, 1984, *Hypopheltes* Cushman, 1924, *Pergaphaga* Gauld, 1984, *Tasmabates* Gauld, 1984, and *Westwoodia* Brullè, 1846. *Catucaba*, *Dictyopheltes*, *Hypopheltes*, *Pergaphaga* and

*Tasmabates* are all monotypic. The Australian genus *Westwoodia* (= *Scolobatina* Roman, 1915) was placed by Townes (1970b) in the separate tribe Westwoodiini together with *Hypopheltes* and “*Megaceria*”. Townes’ (190b) redescription and accompanying illustration of *Megaceria* were based on misidentified specimens of an undescribed genus of Westwoodiini subsequently described by Gauld (1984) as *Pergaphaga*. The true *Megaceria* currently belongs to the tribe Euryproctini of the Ctenopelmatinae, but the general resemblance between *Pergaphaga* and *Megaceria*, including the shared absence of a glymma, lead to the misidentification by Townes (Gauld 1984). Gauld (1984) also sunk Westwoodiini under Scolobatini. The relationships of these groups are reviewed in detail in the Discussion section of Chapter VI.

With the exception of *Tasmabates*, a monotypic genus described from a single specimen from Tasmania, all Australian Scolobatini are extremely large, comparable in size only to two other genera of Ctenopelmatinae, *Opheltes* (Perilissini) and *Megaceria* (Euryproctini). The Australian Scolobatini attack large pergid sawflies, while the Scolobatini in the Palearctic and the New World are considerably smaller, and attack argid sawflies. Size variation among non-Australian Scolobatini is largely restricted to *Physotarsus* – until now the second largest genus of the tribe, while species of *Scolobates* are mostly uniform in size. Coloration and sculpture patterns are extremely diverse in the Scolobatini.

The genus *Physotarsus* is restricted to the Neotropics. Six of the nine described species are known only from Costa Rica (Gauld 1997) and three from Mexico. Estimates as to the relative size of this genus have varied from “moderate” (Gauld 1997) to “rather large” (Townes 1970b), while the range has been estimated as stretching “from southern United States to Argentina” (Townes 1970b). The only available host record for *Physotarsus* is that of *Physotarsus adriani* Gauld, 1997 parasitising the sawfly *Trochophora lobata* (Argidae) in Costa Rica (Janzen, <http://janzen.sas.upenn.edu/Wadults/searchpara.lasso>)

No comparative taxonomic work is available for *Physotarsus* or Scolobatini. A quantitative phylogenetic approach is novel not only to the tribe, but also to Ctenopelmatinae. This study is subdivided into a species revision of *Physotarsus* (Chapters III and V), and a generic revision of Scolobatini (Chapters IV and VI).

## CHAPTER II

### MATERIALS AND METHODS

#### Materials

Most of this study was based on loaned material. Over 950 specimens were borrowed from the following institutions:

ANIC: Australian National Insect Collection, Queensland, Australia

AEI: American Entomological Institute, Gainesville, USA

BMNH: British Museum of Natural History, London, United Kingdom

CNC: Canadian National Collections, Ottawa, Canada

HELLEN: Zoological Museum of Finland, Helsinki, Finland

INBC: Instituto Nacional de Biodiversidad Collection, San Jose, Costa Rica

NMV: National Museum of Victoria, Melbourne, Australia

QM: Queensland Museum, Brisbane, Australia

TAMU: Texas A&M University Entomological Collections, College Station, USA

NMNH: United States National Museum of Natural History, Washington DC, USA

A large part of the New World material was borrowed from the AEI. All newly designated type specimens are labeled as such, and, depending on the availability, up to ten paratypes are designated per species and deposited at the same institution they were borrowed from originally. A list of taxa used in this revision is detailed in the “Taxa” sections of Chapters V and VI, and is the same for both descriptive and analytical sections of this work.

#### Data acquisition and specimen examination

##### *Observations: Whole Specimens*

Light microscopy with magnifications up to 100X was used for morphological observations. Most characters could be observed with direct lighting, with proper



adjustments of the light source however, some ambiguous areas were observed under light scattered through mylar sheets. This applies in particular to smaller and lighter-colored species of *Physotarsus*, some of which have highly transparent cuticle. Dark gray background generously provided by “Home Depot©” was occasionally used to increase contrast. Combined with mylar light scattering, this technique was particularly useful for viewing venation characters.

### *Dissections*

Dissections of some specimens were performed in order to access some internal or retracted structures, such as the mouthparts, antennal tyloids, and eggs. Specimens to be used for mouthpart dissections were first treated with 10% potassium hydroxide (KOH), and then rinsed in 80% ethanol (EtOH). Potassium hydroxide treatment was not applied to the dissections of antennae and abdomen. All dissections were carried out in glycerin, after which specimens were rinsed and preserved in 80% ethanol.

### *Figures*

A large portion of images was acquired digitally using Syncroscopy's AutoMontage® software, in combination with a ProgRes 3008 digital camera mounted on a Leica MZ APO dissecting microscope. All images were further processed using various minor adjustment levels in Adobe Photoshop® Elements® 2.0, such as image cropping, image rotation, adjustment of contrast and brightness levels, and color removal. Environmental Scanning Electron Microscopy (ESEM) was also used to code and illustrate a few morphological characters. Specimens for ESEM were mounted on carbon tape and imaged without coating. Brightness and contrast of the ESEM images were also adjusted in Photoshop® Elements® 2.0. All Auto-montage images are available in color and at high resolution on the web, <http://hymenoptera.tamu.edu/internal>.

### **Description - format and terminology**

Comparative morphological descriptions are accompanied by all available biological and biogeographical data. Higher taxonomic status of taxa delineated in

Chapter IV follows the established classification (Townes 1970 b, Gauld 1997), whereas their taxonomic placement based on the phylogenetic analyses is discussed in the Discussion sections of Chapters V and VI. Species-level revision of *Physotarsus* includes detailed comparative morphological descriptions, and a key to all the species of this genus (Chapter III). Similarly, Chapter IV includes a key and comparative generic descriptions for all Scolobatini. Morphological features used in previous generic characterizations (Townes 1970), Gauld 1984) are reviewed and critically evaluated in the Discussion section of Chapter VI. Morphological terminology is used partially following the most recent taxonomic work on the Ichneumonidae by Ian Gauld (1984, 1997), as well as selectively from H. Townes (1970 b). All morphological terms are defined and illustrated in the morphology section of Chapter II. A detailed treatment of characters and states used in the analyses is presented in chapters V and VI.

Comparative taxonomic descriptions are available for all but one species of *Physotarsus* and all genera of Scolobatini (Chapter III, IV). Comprehensive keys to all species of *Physotarsus* and all genera of Scolobatini are accompanied by character illustrations, which are also available on-line at: <http://hymenoptera.tamu.edu/internal/keys>. Keys are based largely on female specimens, although a few prominent and notable male characters are used.

Species descriptions are formatted as follows: *name*, *nomenclatural history* and *taxonomic status*, *diagnosis*, *head*, *mesosoma*, *metasoma*, *male description*, *color*, *materials examined*, *biological notes*, and *remarks*. Diagnoses are presented as a concise combination of diagnostic characters, as no single character is sufficient to diagnose a species. Diagnoses presented in this study are somewhat more lengthy and detailed as compared to other works on Scolobatini (Gauld 1997). This emphasis is due to the high amount of variation observed among most species, as well as a large number of single specimens representing undescribed morpho-species, all factors that point to the probability of a large number of species yet to be described. Generic descriptions are followed by the *distribution* section, which contains the biogeographic data, a *biology* section, as well as *variation* and *diversity* sections, in which the interspecific variation and species diversity within the genus are discussed. The “materials examined” is arranged in the following order: number of specimens examined, followed by the

holotype and paratype data. Other individual specimen data include sex (♂♀), followed by label locality, date, and (collectors). The “biological notes” section indicates host information (where available). All other relevant data, such as etymology, is provided at the end of the description in the “remarks” section.

No species are described from a single specimen. It is important to note, however, that most specimens used in this study are female, thus no morphological information is available for males of many species of Scolobatini. Invariable characters are reviewed in detail in the General Morphology section of Chapter IV, and are not repeated in descriptions at lower taxonomic levels.

### *Glossary of morphological terminology*

Most of the terminology used in morphological descriptions is adapted after the most recent and detailed work on the Ichneumonidae: “Ichneumonidae of Costa Rica” (Gauld 1997), and “Genera of Ichneumonidae Part III” (Townes 1970 b). Some terms, however, are novel. Following is the overview of main morphological characters in the order head, mesosoma, wings, metasoma, legs.

### *Head (Fig. 1)*

Clypeal margin refers to the ventral-most margin of the clypeus; its shape is quite variable across its width, although the greatest degree of variation is observed in the median part of the clypeal margin. The following states are observed in this region: thin, even margin (Fig. 5), margin somewhat thickened, a distinct rounded or truncate median lobe (Fig. 6) or a distinct median tooth (Fig. 7). The clypeus is quite prominent, delimited by the epistomal suture in some taxa. Intraspecific and interspecific variation is also present in clypeal width-to-length ratio, a character not utilized in phylogenetic analyses due to its continuous nature.

Face is defined as the area between the anterior margin of the toruli and the anterior tentorial pits dorso-ventrally, and is limited by inner eye margins laterally. The face terminates dorsally with an apical tooth, which is located just below the toruli. The area between the mandibular base and the anterior eye margin is the malar space. Areas surrounding the toruli laterally and posteriorly are defined based on their position relative

to the base of the antennae. Inter-antennal and post-antennal areas carry various sculptural features in some Australian taxa. The lateral distance of the torulus to the eye margin also varies among taxa. The widest diameter of the median ocellus is measured in relation to the lateral ocelli, which are also situated at variable distance from each other and the lateral eye margin. Characteristics of size and relative positioning of ocelli carry important descriptive value, but are not very informative phylogenetically. Antennae carry a number of useful characters, such as the antennal tyloid on the lateral part of flagellomere 1, the total number of flagellomeres, and the relative length of flagellomeres 1 and 2. Eyes are quite uniform, oval and bulging to various degrees. The shape of the eye and the degree of its protrusion from the head are quite uniform among taxa, although the eyes are described as “bulging” in a few *Physotarsus* species. The eye measurements are also compared to the length measurements of the first antennal segment: widest transverse diameter of eye refers to the widest horizontal distance between the dorsal and the ventral eye margins. The area behind the eye laterally is referred to as the gena, and is delimited posteriorly by the occipital carina.

Characters of the posterior side of the head are very informative, although less readily accessible. An occipital carina is present in most taxa, but narrowly to widely reduced dorsally in some. If present, the occipital carina terminates at mandibular base. The hypostomal carina is present in all taxa reviewed here, and terminates at the mandibular base, sometimes joining the occipital carina at, or before that juncture. The two carinae can also reach the mandibular base independently. Mouthpart characters are those of the labium and the labial and maxillary palps. Although the number of palpomeres is standard (5-4) in all taxa, their relative length varies. The labium and its components can be greatly elongate, an arrangement referred to as haustellate mouthparts.

### *Mesosoma (Fig. 2)*

Most thoracic characters are on the dorsum or pleuron; the ventral region of ichneumonid wasps is only slightly variable at the sub-familial level. The pronotum varies in both shape and texture. There is variation in the shape of the anterior margin of the pronotum dorsally, as well as in the lateral corner of the pronotum above the

prothoracic spiracle. The lateral groove of the pronotum is sometimes present and is variously deep and wide among taxa. The texture of the pronotum varies from completely glabrous to quite densely punctate. Dorsally, the (meso) scutum may or may not bear notauli, and there is subtle variation in the shape of scutellum. The mesopleuron carries the epicnemial carina, which terminates in a number of different orientations with respect to the anterior margin of the mesopleuron. The dorsal reach of the epicnemial carina is expressed as the proportion of the distance it extends between the ventral most corner of the pronotum and the lateral corner of the pronotum, e.g. “the epicnemial carina reaches 0.3 times the height of pronotum” means that it extends to 0.3 times the overall height of the pronotum from its ventral-most corner. The mesopleuron carries a number of punctational and minor sculptural characters which are used mainly in species taxonomy. The bulk of the mesosomal characters are found on the propodeum. Many taxa have varying degrees of development of the median longitudinal and pleural carinae, as well as the anterior and posterior transverse carinae. There is also notable variation in the sculpture of the median and lateral areas of the propodeum, which are delimited by the pleural carinae (or the approximate position thereof in taxa that lack it).

### *Wings (Fig. 3)*

Color: the majority of taxa described in this work have hyaline, or transparent wings. The coloration may vary, however, darkening gradually with yellowish, orange, and brownish hues. The following terms are used to describe the darker wing colors:

Dusky or Infumate – pale fuscous, light brownish (often refers to forewing apex)

Fuscous – dark brown, approaching black

The amount of pigment in the wing also influences the coloration of the pterostigma and associated wing veins. However, this characteristic is not used in this work due to intraspecific variation in the color of pterostigma.

Vein development: two main types of veins are emphasized here: spectral and tubular veins. Spectral veins are not as distinct as tubular, but are flattened dorso-ventrally, sometimes interrupted, whereas tubular veins are darker, 3-dimensional, and usually uninterrupted.

Venation nomenclature: fore wing: Two cells (areas delimited by wing veins) are used in the descriptive and the analytical portions of this work: the marginal cell and the 1<sup>st</sup> subdiscal cell. The marginal cell is delimited by the Rs+2r vein at the base and the Rs vein at the apex, and anteriorly by the pterostigma and the wing margin. The 1<sup>st</sup> subdiscal cell is adjacent to the posterior wing margin, and is delimited anteriorly by the Cu1 vein, basally by cu-a, and posteriorly by Cu1b apically. For further nomenclature of specific wing veins, see Fig 3. The areolet in the forewing is considered open when vein 3rs-m is absent, and closed when vein 3rs-m is present. The dorsal fusion of veins 2rs-m and 3rs-m is referred to as a petiolate areolet.

Hind wing: one of the most important characters for the taxonomy of Scolobatini is the distal abscissa of vein 1a, and its gradual reduction observed throughout genera. Other veins used in species descriptions are the cubitella and radiella veins, as well as vein Cu1 and its associated abscissae.

#### *Metasoma (Fig. 4)*

Abdominal segments 2-7 display few novel characters in ichneumonids. The tergite of the first abdominal segment (T1) carries the glymma anteriorly between the lateral and median longitudinal carinae. Laterotergites are located at the tergo-sternal juncture along the posterior ½ of the first 3-4 segments, and are membranous in some taxa. Ventrally, sternite 1 (S1) varies in how far it extends along the segment with respect to the spiracle, which is flat to somewhat raised in some taxa.

Apical segments contain genitalia, which are fairly uniform among higher taxa with some variation in the shape of male and female genital plate and the male aedeagus. Cerci are almost always distinguishable, protruding to various degree and covered with setae at their apex. The female ovipositor is distinctly notched and covered by the ovipositor sheath, the shape of which is also quite uniform.

#### *Legs*

The width and length ratio of the trochanter and its apical extension in relation to the anterior margin of the trochantellus proved very useful characters in defining one of the genera of Scolobatini. A small tooth at the apex of foretibia is one of the defining

features of the Ctenopelmatinae. Various features of the tarsal segments are also used in the descriptions, as well as the length of the pretarsus and the type of tarsal claw.

### **Phylogenetic analyses**

Specimens of Scolobatini are fairly rare in collections. Taxonomic sampling for the analyses was, therefore, exhaustive – all available specimens of any particular taxon were utilized in character mapping. Images of all type material are available on the web, on the following database: <http://hymenoptera.tamu.edu/internal>

Not all character states of all taxa used in the analyses are available as an image. The illustrations and descriptions presented in chapters V and VI, however, should allow for an unambiguous interpretation of character states.

#### *Coding Morphological Characters*

Most characters used in this study have been utilized in previous morphological descriptions of Ichneumonidae in general and Ctenopelmatinae in particular, whereas a few are entirely novel. Conversely, a few characters previously considered taxonomically informative are excluded. Each character was examined across all taxa of Scolobatini in order to clearly divide it into definable states. Character coding was performed using up to 5 male and female specimens, where available. Different sets of characters were used in the analyses of intra-generic relationships of *Physotarsus* and the generic revision of Scolobatini. No biological characters were employed. Though some authors favor the use of biological characters in phylogenetic analysis, such data are lacking for most Scolobatini (Wenzel 1992).

#### *Parsimony Analyses*

Matrices are analyzed with heuristic search methods using WinClada® (WinClada 2002). All characters are treated as unordered, and no transformation series are implied by character state number. The first set of analyses includes 30 characters and 34 OTUs (Table 2), and the second set includes 25 characters and 31 OTUs (Table 6), with no character weighting employed in either part of the analyses. No specific

specimen vouchers were designated. Preexisting and newly-designated primary type and paratype material was used in coding where available. Topologies used in both analyses were obtained using a heuristic search with 10,000 replications, 5,000 trees kept.



### CHAPTER III

#### REVISION OF *PHYSOTARSUS* TOWNES, 1966

##### Overview of *Physotarsus* Townes, 1966

##### *Physotarsus* Townes, 1966

*Physotarsus* Townes, 1966. Type species: *Tryphon maculipennis* Cresson, 1874, by original designation. Townes (1970 b): copy of original description. Carlson (1979): catalog. Gauld (1997): revision of *Physotarsus* of Costa Rica; detailed redescription of genus, as well as illustrated descriptions of 6 new species from Costa Rica. Yu and Horstmann (1997): catalog.

*Physotarsus* is derived from the Greek φουσκώνω [inflate] plus τάρσος [part of foot] in reference to the inflated hind tarsus of a male (Townes, 1966).

*Description.* – Length: body 3.5-9.7 mm, fore wing 3.2-10.4 mm. Clypeal margin shape varies. Clypeus 2.4-4.0 as wide as long, weakly convex in profile, sometimes separated medially by a weak transverse ridge, without a median tooth. Anterior tentorial pits oval to slightly elongate with lateromost corners pointed laterad or upcurved. Malar space 0.2-0.8 times basal width of mandible base, mandible with lower tooth slightly longer than upper, mandible tapering over basal 1/3 to 1/2, almost parallel-sided apically. Dorsal margin of mandible without a distinct median convexity. Face smooth to quite strongly punctured, 1.2 to 2.3 times as wide as long, with a median tooth dorsally. Interantennal area flat to slightly concave, anterior margin of torulus situated at about 0.6-0.8 of eye height. Widest diameter of torulus 1.0-1.6 times widest diameter of median ocellus. Area between lateral ocelli flat to strongly depressed, distance between lateral ocelli 0.4-1.5 times their widest diameter, distance from lateral ocellus to the eye margin 1.4-2.8 times widest diameter of lateral ocellus. Area behind ocelli regularly rounded to sharply declivitous. Antennae quite long, number of flagellomeres varies from 22 to 47. First flagellomere with a small tyloid laterally, flagellomere length 0.7-1.6 times widest

transverse diameter of eye, second flagellomere 0.4-0.8 times length of first. Occipital carina present, incomplete, reaching the ventral 0.2 to 0.8 of head, never joining hypostomal carina at or before mandibular base. Pronotum broadly rounded to truncate anteriorly, flat to quite strongly emarginate medially, lateral margin upcurved. Lateral groove of the pronotum absent to complete, its width ventrally variable. Pronotum glabrous to variably punctured, sometimes partially rugose. Scutum glabrous to densely punctate, notauli absent. Epicnemial carina extending along ventral 0.2-0.4 of posterior margin of pronotum, sometimes turned towards but never reaching anterior margin of mesopleuron. Mesopleuron always lightly pubescent ventrally, smooth to densely punctate laterally. Propodeum with pleural carinae sometimes present to complete, median longitudinal carinae sometimes present as posterior vestiges. Punctuation variable, medial punctures absent posteromedially, sometimes present anteromedially; lateral punctuation always denser than medial. Posterolateral edge of propodeum somewhat upcurved. Trochanter less than 3.0 times as long as basally wide, apical margin of trochanter reaching apical margin of trochantellus. Pretarsus longer than tarsomere 4. Claws basally toothed to almost fully pectinate. Forewing with abscissa of Cu1 between 1m-cu and Cu1a about 0.35-1.0 times length of Cu1b. Marginal cell about 2.5-3.3 times as long as wide. Hind wing with distal abscissa of 1A entirely absent. Tergite 1 about 1.5-2.4 times as long as broad, spiracles sometimes slightly protruding in profile. Cerci sessile to quite prominent.

*Color* – extremely variable. Wings largely hyaline, although yellow and fuscous colors observed in some species.

*Distribution* – restricted to the New World, occurring from S. USA to Argentina.

*Biology* – species of *Physotarsus* are larval-prepupal parasitoids of Argidae sawflies. Only one host record actually exists: *Physotarsus adriani* Gauld 1997 was reared from the pupae of the sawfly *Trochophora lobata* (Argidae) in Costa Rica (Janzen, web). The only record of a live [male] parasitoid states that it was observed to “have a behavior of a housefly – buzzing flight” (Janzen, web). Parasitoids were recorded as emerging from the sawfly pupae on November 7, which is the end of the rainy season in Costa Rica, a time of the year characterized by cool temperatures.

*Interspecific variation* – *Physotarsus* species generally vary widely in size, color patterns, and the extent of pubescence and punctuation. Other characters useful for differentiating species are found on the hind wings and the hind legs.

*Diversity* – this genus is quite large (Table 1). During the course of this study, 44 additional morpho-species, each represented by a single specimen, were encountered.

**TABLE 1: Checklist of the *Physotarsus* Species**

| Species of <i>Physotarsus</i> described prior to this work  | Species of <i>Physotarsus</i> described in this work   |
|---|--|
| <i>P. adrianni</i> Gauld, 1997<br><i>P. bonillai</i> Gauld, 1997<br><i>P. castilloi</i> Gauld, 1997<br><i>P. eliethi</i> Gauld, 1997<br><i>P. fabioi</i> Gauld, 1997<br><i>P. maculipennis</i> (Cresson, 1874)<br><i>P. montezuma</i> (Cameron, 1886)<br><i>P. varicornis</i> (Cameron, 1886) | <i>P. albus</i><br><i>P. claviger</i><br><i>P. concavus</i><br><i>P. cordatus</i><br><i>P. emarginatus</i><br><i>P. flavipennis</i><br><i>P. foveatus</i><br><i>P. gineus</i><br><i>P. glabellus</i><br><i>P. laucos</i><br><i>P. luteus</i><br><i>P. melipennis</i><br><i>P. melotarsus</i><br><i>P. niveus</i><br><i>P. oculatus</i><br><i>P. tonicus</i><br><i>P. truncatus</i> |

***Physotarsus* Townes, 1966: key to species**

(*P. montezuma* (Cameron, 1886) is not included in the key due to the inaccessibility of the type specimen by the author)

- 1 Fore wing weakly to strongly yellowish or brown to black at base, with or without infumate areas apically.....2
- 1' Fore wing hyaline at base.....8

|       |   |  |
|-------|---|--|
| 2(1)  | Fore wing evenly colored, entirely infumate or pale yellowish-brown.....                                | 3                                      |
| 2'    | Fore wing not evenly colored.....   | 4                                      |
| 3(2)  | Fore wing pale yellowish-brown.....   | <i>P. albus</i> Zhaurova, 2006         |
| 3'    | Fore wing entirely brownish-infumate.....   | <i>P. melipennis</i> Zhaurova, 2006    |
| 4(2)  | Basal part of fore wing brown to black, apical part variable.....                                       | 5                                      |
| 4'    | Basal part of fore wing yellowish, apex infumate.....   | 6                                      |
| 5(4)  | Fore wing with two sub-apical yellowish spots or bands; hind femur and tibia orange.....                | <i>P. maculipennis</i> (Cresson, 1874) |
| 5'    | Fore wing with a single subapical yellowish spot or band; hind femur and tibia black.....               | <i>P. varicornis</i> (Cameron, 1886)   |
| 6(4)  | Mesosoma with yellow and black markings, face quite densely punctate medially (Fig. 34 ).....           | <i>P. flavipennis</i> Zhaurova, 2006   |
| 6'    | Mesosoma entirely yellowish to light orange, face very lightly evenly punctate (Fig. 29 ).....          | 7                                      |
| 7(6)  | Frons and first tarsomere of the hind leg orange.....   | <i>P. adriani</i> Gauld, 1997          |
| 7'    | Frons and first tarsomere of the hind leg black.....  | <i>P. castilloi</i> Gauld, 1997        |
| 8(1)  | Epicnemial carina strongly turning towards the anterior margin of mesopleuron, but not reaching it..... | 9                                      |
| 8'    | Epicnemial carina parallels the anterior margin of mesopleuron.....                                     | 12                                     |
| 9(8)  | First metasomal tergite entirely yellow.....  | <i>P. eliethi</i> Gauld, 1997          |
| 9'    | First metasomal tergite with brownish markings.....   | 10                                     |
| 10(9) | First tergite white anteriorly, brown posteriorly.....  | <i>P. niveus</i> Zhaurova, 2006        |

|        |  |                                    |
|--------|--|------------------------------------|
| 10'    | First tergite entirely brown.....  | 11                                 |
| 11(10) | Face entirely white; hind femur dark brown.....  | <i>P. laucos</i> Zhaurova, 2006    |
| 11'    | Face yellow; hind femur yellowish orange.....  | <i>P. glabellus</i> Zhaurova, 2006 |
| 12(8)  | Ventral clypeal margin with a prominent angulate central lobe (Fig. 7).....                                | 13                                 |
| 12'    | Ventral clypeal margin not as above.....   | 15                                 |
| 13(12) | Body entirely yellowish-orange with no brown or black markings<br>.....                                    | <i>P. bonillai</i> Zhaurova, 2006  |
| 13'    | Body not colored as above; brown or black markings distinct.....   | 14                                 |
| 14(13) | Scutum and face with brown markings; propodeum entirely brown<br>.....                                     | <i>P. claviger</i> Zhaurova, 2006  |
| 14'    | Scutum and face white to light yellowish; propodeum white with two brownish<br>spots anterolaterally.....  | <i>P. oculatus</i> Zhaurova, 2006  |
| 15(12) | Face, mesosoma, fore and middle legs entirely yellowish<br>.....   | <i>P. luteus</i> Zhaurova, 2006    |
| 15'    | Color variable, combination of characters not as above.....  | 16                                 |
| 16(15) | Face quite strongly protruding medially (Figs. 55,56).....   | 17                                 |
| 16'    | Face not to very weakly protruding in profile (Fig. 25).....   | 20                                 |
| 17(16) | Scutum largely impunctate posteriorly, anterior punctures very sparse<br>.....                             | <i>P. gineus</i> Zhaurova, 2006    |
| 17'    | Scutum punctate posteriorly, punctures dense.....  | 18                                 |
| 18(17) | Scutum black with two small pale-yellowish spots laterally; fore and middle<br>femora partially black..... | <i>P. tonicus</i> Zhaurova, 2006   |

- 18' Scutum black with two elongate pale-yellowish spots laterally and lateromedially; fore and middle femora yellowish.....19
- 19(18) Mesopleuron entirely black; face yellowish laterally, black medially  
.....*P. foveatus* Zhaurova, 2006
- 19' Mesopleuron black with yellow markings; face entirely yellowish  
..... *P. melotarsus* Zhaurova, 2006
- 20(16) Metasomal tergite 2 entirely orange; mesopleuron almost entirely black.....21
- 20' Metasomal tergite 2 brownish laterally, orange medially; mesopleuron largely yellowish with a black stripe.....22
- 21(20) Scutum with a narrow anterolateral yellow margin (Fig 23); male subgenital plate deeply emarginate, cordate (Fig. 26) .....*P. cordatus* Zhaurova, 2006
- 21' Scutum with anterolateral margin black (Fig 61); male subgenital plate deeply emarginate, inner margin not emarginate (Fig. 60).....*P. truncatus* Zhaurova, 2006
- 22(20) Tarsomeres 3 and 4 dark orange to brownish; male genital plate deeply emarginate, even (Fig. 32).....*P. emarginatus* Zhaurova, 2006
- 22' Tarsomeres 3 and 4 yellowish, much lighter than tarsomeres 1, 2 and 5; male genital plate slightly emarginate (Fig. 23).....*P. concavus* Zhaurova, 2006

### ***Physotarsus* Townes, 1966: species descriptions**

#### ***Physotarsus adrianni* Gauld, 1997**

(Figs. 9,10)

*Physotarsus adriani* Gauld, 1997, pp. 194-195. *Physotarsus adriani*: Yu & Horstmann 1997: catalog, pp. 455 .

*Diagnosis* – Lateral ocelli separated by 0.4-0.6 times their widest diameter from each other, and by about 1.8-2.1 times their widest diameter from the eye margin. Antenna with 30-32 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 2.0 times as long as broad, spiracles protruding in profile. Head brownish-orange, face mostly brown. Mesosoma and metasoma orange. Hind legs orange, tarsus distally infusate. Fore wing very strongly yellowish proximally, blackish infumate distally.

*Description: Female* – Body (Fig. 9) 4.8-6.2 mm, fore wing 4.6-7.0 mm. Head (Fig. 10): Clypeal margin widely truncate laterally, with a thick, somewhat angulate central lobe. Clypeus about 3.6 times as wide as long, divided medially by a shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.4-0.5 times width of mandibular base. Face 1.3 times as broad as long, quite flat, evenly sparsely punctured. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.3 times widest diameter of median ocellus. Lateral ocelli separated by 0.4-0.6 times their widest diameter from each other, and by about 1.8-2.1 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli sharply declivitous. Antenna with 30-32 flagellomeres, length of first flagellomere 1.4 times widest transverse diameter of eye, second flagellomere 0.7-0.8 times length of first. Occipital carina present on the posterior 0.2-0.3 of head. Mesosoma: Anterior margin of pronotum medially slightly emarginate, laterally rounded and upcurved. Lateral groove of the pronotum vestigial, present on the dorsal 0.1, sometimes absent entirely. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.55-0.65 times length of Cu1b. Marginal cell about 2.6-2.9 times as long as wide. Propodeum without carinae, impunctate medially, pubescent laterally. Claws simple. Metasoma: T1 about 2.0 times as long as broad, spiracles protruding in profile; cerci prominent, not protruding.

*Male* – similar to female in structure and color; subgenital plate with a very broad U-shaped incision in posterior margin.

*Color:* Head brownish-orange, face mostly brown. Antennae black. Mesosoma and metasoma orange, ventrally grading to yellowish. Fore and middle legs yellowish; hind legs orange, with tarsus distally infusate. Fore wing very strongly yellowish proximally, blackish infumate distally; pterostigma usually orange-brown, rarely blackish.

*Material Examined* – paratypes: Costa Rica: Guanacaste Prov.: 7 ♀, Santa Rosa National Park, 300m, vi-vii.1976-7 (Janzen) (AEIC, NHM);

*Biological Notes* – *Physotarsus adriani* is the most frequently collected species in the genus in Costa Rica, although it has only been taken in north-western Guanacaste in seasonally dry forests. All specimens have been collected in June and July, shortly after the start of the wet season, though rearing suggests adults are about in late May, and there could be a second generation in November. This species has also been recorded from Brazil. Host record from Dr. Dan Janzen's biodiversity website: <http://janzen.sas.upenn.edu/Wadults/searchpara.lasso>. Voucher code: 88-SRNP-67. "Comments on caterpillar: large plant with large burst of new foliage, lots of larvae (of host *Trochophora lobata* (Argidae) on foliage, the small hard silk cocoon spinner, saw one male parasitoid flying in foliage of plant - has behavior of a house fly, buzzing flight; on 27-29 May they spun; just before spin, walk up side of plastic bag and leave a small white clear foam patch, then go back down into the litter to spin; 3 sawflies eclosed 11 June 1988, ETOH 2 last instar larvae, put cocoons in dry container, in November eclosed 7 yellow and black small ichneumonids, one from each cocoon, cut round hole through side of cocoon; these wasps are all paratypes"

*Remarks* – Gauld (1997) reported additional material: Holotype ♀, Costa Rica, Guanacaste Prov., Guanacaste National Park, Finca Jenny, 300 m, vi. 1990 (*Biodiversity survey*) (INBio). Paratypes: Costa Rica: Guanacaste Prov.: 2 ♂, 7 ♀, Santa Rosa National Park, 300m, vi-vii.1976-7 (Janzen) (AEIC, NHM); 1 ♀, same locality, in Bosque Hymedo, vi-vii.1990 (*Biodiversity Survey*) (INBio, NHM). 1 ♀, Tucurui, Para, Brazil (M. Alvarenga).



***Physotarsus albus* Zhaurova, spec. nov.**

(Figs. 11,12)

*Diagnosis* – Lateral ocelli separated by about 0.5 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Antenna with 24-26 flagellomeres. Pronotum and scutum impunctate, shiny. T1 3.0 times as long as broad, spiracles protruding in profile. Face white; frons and occiput orange. Mesosoma orange, area around propodeal spiracles sometimes brown. Metasomal tergites brown with very thin, white lateral and apical margins, sternites white. Hind leg dark-brown to black. Fore wing hyaline with a light brown tip.

*Description: Male* – Body (Fig. 11) 5-5.5 mm, fore wing 5-5.4 mm. Head (Fig. 12): Clypeal margin widely rounded laterally, with a thick somewhat angulate central lobe. Clypeus about 3.0 times as wide as long, not divided medially by a shallow transverse depression. Clypeus, mandibles and face covered by sparse long setae. Anterior tentorial pits oval. Malar space 0.6-0.8 times width of mandibular base. Face about 1.5-1.6 times as broad as long, smooth, impunctate. Interantennal area slightly concave, area immediately behind antenna weakly concave, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.1 times widest diameter of median ocellus. Lateral ocelli separated by about 0.5 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Area between lateral ocelli flat to slightly depressed, area behind ocelli sharply declivitous. Antenna with 24-26 flagellomeres, length of first flagellomere about equal widest transverse diameter of eye; second flagellomere about 0.7 times length of first. Occipital carina present on the ventral 0.4 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally truncate and strongly upcurved. Lateral groove of the pronotum absent entirely or present vestigially on dorsal 0.1. Pronotum and scutum impunctate, shiny. Epicnemial carina turning towards the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 length of Cu1b.

Marginal cell about 2.8 times as long as wide. Propodeum with posterior vestiges of median longitudinal and pleural carinae, impunctate medially, sparsely punctate laterally. Metasoma: T1 3.0 times as long as broad, spiracles protruding in profile. Male subgenital plate prominent, its margin even.

*Female* – none

*Color* – face white, frons and occiput orange. Antennae dark-brown to black. Mesosoma orange, area around propodeal spiracles sometimes brown. Metasomal tergites brown with very thin white margins, sternites white. Fore and middle legs yellowish, apex sometimes dark; hind leg dark-brown to black. Fore wing entirely pale yellowish-brown.

*Material Examined* – 10 males. Holotype: ♂, Serra da Bocaina, 1600m. S.J. Barrieros, Brazil, 4-7-XI-1967, (Alvarenga & Seabra); Paratypes: 1 paratype ♂ with same label as holotype; 8 ♂, S.J. Barrieros, Serra da Bocaina, 1650m, Brazil, XI-1968, (Alvarenga & Seabra).

*Biological Notes* – host unknown, species found in highlands at 1600-1650m.

*Remarks* – *albus* is Latin for white.

### ***Physotarsus bonillai* Gauld, 1997**

(Figs. 13,14)

*Physotarsus bonillai* Gauld, 1997, pp. 195-196; *Physotarsus bonillai*: Yu & Horstmann, 1997: catalog, p. 455.

*Diagnosis* – lateral ocelli separated by 0.7-0.8 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Antennae with 26-27 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 1.5 times as long as broad, spiracles protruding in profile. Head entirely pale yellowish. Mesosoma and metasoma yellowish. Hind legs orange, with tarsus uniformly infusate. Fore wing hyaline, apex infumate.

*Description: Female* – body (Fig. 13) 4.3-5.0 mm, fore wing 3.5-5.0 mm. Head (Fig. 14): Clypeal margin widely truncate laterally, with a thick, somewhat angulate

central lobe. Clypeus about 3.8 times as wide as long, divided medially by a shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.5-0.6 times width of mandibular base. Face 1.8 times as broad as long, quite flat, evenly sparsely punctured. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.2 times widest diameter of median ocellus. Lateral ocelli separated by 0.7-0.8 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli sharply declivitous. Antennae with 26-27 flagellomeres; length of first flagellomere 1.1 times the widest transverse diameter of eye, second flagellomere 0.6-0.7 times the length of first. Occipital carina present on the ventral 0.2-0.3 of head. Mesosoma: Anterior margin of pronotum medially slightly emarginate, laterally rounded and upcurved. Lateral groove of the pronotum present on the dorsal 0.4. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.35-0.55 times length of Cu1b. Marginal cell about 2.6-2.8 times as long as wide. Propodeum with a vestige of pleural carina, impunctate medially, pubescent laterally. Claws basally pectinate. Metasoma: T1 about 1.5 times as long as broad, spiracles protruding in profile; cerci prominent.

*Male* – subgenital plate with a narrow V-shaped incision in posterior margin. Similar to female structure and color.

*Color* – head entirely pale yellowish; antenna with scape and pedicel ventrally yellow, infusate dorsally. Flagellum proximally yellowish brown, darker dorsally, grading to entirely black apically. Mesosoma and metasoma pale yellowish. Fore and middle legs yellowish, hind legs orange, with tarsus uniformly infusate. Fore wing hyaline, apex infumate; pterostigma black.

*Material Examined* – paratypes: Costa Rica: Guanacaste Prov.: 1 ♂, 6 ♀, Santa Rosa National Park, vi-x. 1985-7 (Gauld & Janzen) (INBio, NHM).

*Biological Notes* – *Physotarsus bonillai* has only been collected in Costa Rica where several individuals have been taken in Malaise traps operating in dry forests in northwestern Guanacaste. In the intensive sampling programme conducted in Santa Rosa specimens were only taken in very young, regenerating scrub forest west of the Area Administrativa between June and October, the wet season. Two specimens in the AEIC were collected on a dry hill in Santa Rosa in December. A female was collected near Ciudad Colon. Its host is unknown.

*Remarks* – Gauld (1997) reported additional specimens: Holotype ♀, Costa Rica, Guanacaste Prov., Santa Rosa National Park, 300 m, viii. 1985 (Gauld & Janzen) (INBio). Paratypes: Costa Rica: Guanacaste Prov.: 2 ♀, Santa Rosa National Park, vi-x. 1985-7 (Gauld & Janzen) (INBio, NHM); 2 ♀, same locality, dry hill, xii. 1977 (Janzen) (AEIC); San Jose Prov.: 1 ♀, Finca San Luis, nr Ciudad Colon, 800 m, vi-vii. 1990 (Gauld & Hanson) (NHM).

***Physotarsus castilloi* Gauld, 1997**

(Figs. 15, 16)

*Physotarsus castilloi* Gauld, 1997. *Physotarsus castilloi*: Yu & Horstmann, 1997: catalog.

*Diagnosis* – lateral ocelli separated by 0.5-0.6 times their widest diameter from each other, and by about 1.6-1.7 times their widest diameter from the eye margin. Antenna with 30-32 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 2.0 times as long as broad, spiracles protruding in profile. Head orange-brown with face centrally infusate and vertex entirely black. Mesosoma and metasoma orange, ventrally grading to yellowish. Hind legs orange with coxa and trochanter distally infusate, tarsus entirely black. Fore wing very strongly yellowish, distally blackish infumate. Stigma black.

*Description: Female* – body (Fig. 15) 5.0-5.7 mm, fore wing 5.3-6.0 mm. Head (Fig. 16): Clypeal margin widely truncate laterally, with a thick, somewhat angulate central lobe. Clypeus about 4.0 times as wide as long, divided medially by a transverse

depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.3-0.4 times width of mandibular base; Face 1.4 times as broad as long, quite flat, evenly sparsely punctured. Interantennal area slightly concave, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.1 times widest diameter of median ocellus. Lateral ocelli separated by 0.5-0.6 times their widest diameter from each other, and by about 1.6-1.7 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli sharply declivitous. Antenna with 30-32 flagellomeres; length of first flagellomere 1.3 times the widest transverse diameter of eye, second flagellomere 0.6 times the length of first. Occipital carina present on the ventral 0.2-0.3 of head. Mesosoma: Anterior margin of pronotum medially slightly emarginate, laterally rounded and upcurved. Lateral groove of the pronotum, present on the dorsal 0.2. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.6-0.7 times length of Cu1b. Marginal cell about 2.5-2.6 times as long as wide. Propodeum with a vestige of pleural carina, impunctate medially, pubescent laterally. Claws basally pectinate. Metasoma: T1 about 2.0 times as long as broad, spiracles protruding in profile; cerci not protruding.

*Male* – subgenital plate with a very broad but basically V-shaped incision in posterior margin. Similar to female structure and color.

*Color* – head orange-brown with face centrally infusate and vertex entirely black. Antenna entirely black. Mesosoma and metasoma orange, ventrally grading to yellowish. Anterior two pairs of legs yellowish, hind legs orange with coxa and trochanter distally infusate, tarsus entirely black. Fore wing very strongly yellowish, distally blackish infumate; pterostigma black.

*Material examined* – paratypes: Costa Rica: Puntarenas Prov.: 1 ♀, Golfo Dulce Forest Reserve, 24km W of Pan American Highway on road to Rincon de Osa, 100 m, iii-iv.1989 (Gauld) (NHM); 1 ♂, Golfo Dulce Forest Reserve, 24km W of Pan American Highway on road to Rincon de Osa, 200 m, ii.1990 (Gauld) (NHM).

*Biological Notes* – *Physotarsus castilloi* has only been taken in Costa Rica. All specimens were collected in Malaise traps operating in dense primary wet forest in the Golfo Dulce Forest Reserve. It is the only species of the genus that has been collected in such a wet forest locality on the Pacific plain, although *P. eliethi* inhabits similar wet forest on the Atlantic watershed. Its host is unknown.

*Remarks* – Gauld (1997) reported an additional specimens: Holotype ♀, Costa Rica, Puntarenas Prov., Golfo Dulce Forest Reserve, 24km W of Pan American Highway on road to Rincon de Osa, 200 m, viii.1989 (Gauld) (INBio).

***Physotarsus claviger* Zhaurova, spec. nov.**

(Figs. 17-20)

*Diagnosis* – lateral ocelli separated by about 0.7 times their widest diameter from each other, and by 1.7 times their widest diameter from the eye margin. Antenna with 28 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 1.7 times as long as broad. Head yellow, face with a median longitudinal dark-brown stripe. Mesosoma yellow with black markings. Metasomal tergites largely black with a thin yellow apical trim, sternites yellow. Hind femur black, tibia largely yellow with dark apex, tarsi yellow, pretarsus black. Fore wing hyaline, tip fuscous.

*Description: Male* – body (Fig. 17) 5.0 mm, fore wing 5.7 mm. Head (Fig. 18): Clypeal margin widely truncate laterally with a thick, angulate central lobe (Fig. 20). Clypeus about 2.7-3.0 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face sparsely covered by moderately long setae. Anterior tentorial pits deep, elongate and pointed laterally. Malar space about 0.6 times width of mandibular base. Face 2.0 times as broad as long, flat, evenly sparsely punctate. Interantennal area flat, area immediately behind antennae weakly concave turning convex laterally before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.5 times widest diameter of median ocellus. Lateral ocelli are separated by about 0.7 times their widest diameter from each other, and by 1.7 times their widest diameter from the eye margin. Area between lateral ocelli slightly

depressed, area immediately behind ocelli not sharply declivitous. Antenna with 28 flagellomeres, length of first flagellomere 1.6 times widest transverse diameter of eye, second flagellomere 0.7 times the length of first. Occipital carina present on the proximal 0.3-0.4 of head. Mesosoma: Anterior margin of the pronotum medially slightly emarginate, laterally rounded and slightly upcurved. Lateral groove of the pronotum vestigial, present on the dorsal 0.3. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.8 the length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with pleural carinae complete, widely impunctate medially, sparsely pubescent and somewhat rugose laterally. Claws basally pectinate. Metasoma: T1 about 1.7 times as long as broad. Cerci protruding. Subgenital plate narrowly emarginate, fairly deep, its margin even. Aedeagal margin toothed laterally (Fig. 19).

*Female* – none

*Color* – head yellow, face with a median longitudinal dark-brown stripe.

Antennae yellow with a black tip. Mesosoma yellow with black markings. Metasomal tergites largely black with a thin yellow trim, sternites yellow. Fore and middle legs yellow, hind femur black, tibia largely yellow with dark apex, tarsi yellow, pretarsus black. Fore wing hyaline, tip fuscous.

*Material Examined* – 2 males. Holotype: ♂, Villa Nagues, Argentina, 01-I-1966, (H&M Townes); Paratype: ♂, same label as holotype.

*Biological Notes* – host unknown.

*Remarks* – *claviger*: Latin for club bearing. Referring to shape of clypeal margin

***Physotarsus concavus* Zhaurova, spec. nov.**

(Figs. 21-23)

*Diagnosis* – lateral ocelli separated by 1.1-1.2 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin.

Antennae with 33-42 flagellomeres. Pronotum completely glabrous. Scutum shiny, very

sparse punctures present on the anterior 0.3. T1 about twice as long as broad. Head yellow with a black median stripe running down the vertex. Mesosoma black and yellow (Fig. 17). T1 yellow basally with two black spots on the posterior 0.7; rest of tergites largely dark, some with yellow trim apically. Hind femur, tibia and tarsomeres 1 and 2 orange, tarsomeres 3 and 4 usually yellow, sometimes only on one side. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 21) 4.2-5.9 mm, fore wing 3.8-5.3 mm. Head (Fig. 22): Clypeal margin thick, evenly rounded laterally with a thick rounded central lobe. Clypeus about 2.6-2.7 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face covered by very short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.4-0.5 times width of mandibular base. Face 1.8-1.9 times as broad as long, slightly protruding in profile. Face punctures sparse laterally, denser anteromedially. Interantennal area flat, area immediately behind antennae weakly concave laterally turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.3 times widest diameter of median ocellus. Lateral ocelli are separated by 1.1-1.2 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area immediately behind ocelli not sharply declivitous. Antennae with 33-42 flagellomeres; length of first flagellomere 1.3 times widest transverse diameter of eye; second flagellomere 0.6-0.7 times the length of first. Occipital carina present on the proximal 0.6 of head. Mesosoma: Anterior margin of the pronotum medially very slightly emarginate, laterally rounded, slightly upcurved. Lateral groove of the pronotum quite strong, extending to the dorsal 0.8, sometimes complete. Pronotum completely glabrous, impunctate. Scutum shiny, very sparse punctures present on the anterior 0.3. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron punctate, with a prominent shiny spot. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.5-0.6 the length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with at least a posterior vestige of pleural carina present, impunctate medially, moderately densely punctate and



pubescent laterally. Claws basally pectinate. Metasoma: T1 about twice as long as broad. Cerci not protruding.

*Male* – subgenital plate not emarginate, its margin even (Fig. 23). Aedeagal margin not toothed. Similar to female structure and color.

*Color* – head yellow with a black stripe running down the vertex, originating as low as the apical tooth of the frons. Antennae with 3-4 yellowish flagellomeres subapically. Occiput black. Mesosoma black and yellow. First tergite of metasoma yellow basally with two black spots on the distal 0.7; rest of tergites largely dark, some with yellow trim; cerci light-brown. Hind femur, tibia orange, tarsomeres 3 and 4 usually yellow, sometimes only on one side. Fore wing entirely hyaline.

*Material Examined* – I have examined 27 females and 18 males. Holotype: ♀, Portal, AZ, USA, 03-IX-1974, (H&M Townes); Paratypes: 2 ♀, Portal, AZ, USA, 01-07-IX-1974, (H&M Townes); 2 ♀, Portal, AZ, USA, 13-31-VIII-1974, (H&M Townes), 1 ♂, San Pedro Iturbide, 32km W. Linares, Mexico, 6-X-1962, (H&M Townes), 1 ♂, Portal, AZ, USA, 02-05-IX-1974, (H&M Townes); 2 ♂, Portal, AZ, USA, 12-31-VIII-1974, (H&M Townes).

*Biological Notes* – host unknown.

***Physotarsus cordatus* Zhaurova, spec. nov.**

(Figs. 24-27)

*Diagnosis* – lateral ocelli separated by 1.3 times their widest diameter from each other, and by about 2.2 times their widest diameter from the eye margin. Antennae with 36-38 flagellomeres. Pronotum glabrous medially around and below the epomia, punctate anterolaterally. Scutum shiny, very sparse punctures present on the anterior 0.4. T1 about twice as long as broad. Head yellow with a black median stripe on frons and vertex. Mesosoma black and yellow dorsally (Fig. 23). T1 yellow basally with two black spots on the distal 0.7 laterally. Metasoma otherwise uniformly orange. Hind femur, tibia, tarsi and pretarsus uniformly orange. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 24) 5.6 mm, fore wing 5.3 mm. Head (Fig. 25): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus

about 2.8 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.4-0.5 times width of mandibular base. Face twice as broad as long, slightly protruding in profile, terminating dorsally with a median tooth. Face punctures sparse laterally, denser anteromedially. Interantennal area flat, area immediately behind antennae weakly concave laterally turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus 1.3 times widest diameter of median ocellus. Lateral ocelli separated by 1.3 times their widest diameter from each other, and by about 2.2 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed; area immediately behind ocelli not sharply declivitous. Antennae with 36-38 flagellomeres, length of first flagellomere 1.3 times widest transverse diameter of eye, second flagellomere 0.6 times the length of first. Occipital carina present on the ventral 0.6-0.7 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally rounded, slightly upcurved. Lateral groove of the pronotum quite strong, extending to dorsal 0.6. Pronotum glabrous medially around and below the epomia, punctate anterolaterally. Scutum shiny, very light punctures present on the anterior 0.4 (Fig. 27). Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron quite densely punctate ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 the length of Cu1b. Marginal cell about 3.2 times as long as wide. Propodeum without carinae; impunctate and glabrous medially, moderate to dense punctures and pubescence present laterally. Claws simple. Metasoma: T1 about twice as long as broad. Cerci protruding.

*Male* – subgenital plate with wide, deep, truncate median incision, its margin slightly bifurcate (Fig. 26). Aedeagal margin not toothed. Similar to female structure and color.

*Color* – head yellow with a black stripe running down the vertex, originating as low as the apical tooth of face. Antennae darker at the base, gradually becoming lighter in the middle. Occiput black. Mesosoma black and yellow dorsally (Fig. 27). T1 yellow

basally with two black spots on the lower lateral 0.7. Metasoma uniformly orange, cerci dark. Hind femur, tibia, tarsi and pretarsus uniformly orange. Fore wing entirely hyaline.

*Material Examined* – I have examined 1 female and 6 males. Holotype ♂, Valentine Refuge, NE, USA, 04-VI-1972, (H&M Townes). Paratypes: 1 ♀, Valentine Refuge, NE, USA, 08-VI-1972, (H&M Townes); 4 ♂, Valentine Refuge, NE, USA, 05-08-VI-1972, (H&M Townes).

*Biological Notes* – host unknown.

*Remarks* – *cordatus* is Latin for heart-shaped excavation in male genital plate.

### ***Physotarsus eliethi* Gauld, 1997**

(Figs. 28, 29)

*Physotarsus eliethi* Gauld, 1997. *Physotarsus eliethi*: Yu & Horstmann, 1997: catalog.

*Diagnosis* – lateral ocelli separated by 1.6 times their widest diameter from each other, and by 0.9-1.1 times their widest diameter from the eye margin. Antenna with 24 flagellomeres. Pronotum completely glabrous, scutum shiny, impunctate. T1 about 2.3 times as long as broad. Head dark-yellowish, area around ocelli brownish. Body yellowish, abdominal terga 2-8 brownish, hind tibia brown, fore wing hyaline, tip brownish.

*Description: Female* – body (Fig. 28) 3.0 mm, fore wing 4.0 mm. Head (Fig. 29): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 3.3 times as wide as long, not divided medially by a transverse depression. Anterior tentorial pits elongate, pointed laterad. Malar space 0.7 times the width of mandibular base. Face 1.6 times as broad as long, impunctate, rounded in profile. Interantennal area flat, area immediately behind antennae weakly concave laterally turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.6 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of median ocellus slightly smaller than widest diameter of torulus. Lateral ocelli separated by 0.9-1.1 times their widest diameter from each other, and by 1.6 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area

immediately behind ocelli not sharply declivitous. Antenna with 24 very slender flagellomeres; length of first flagellomere 1.4 times the widest transverse diameter of eye; second flagellomere 0.7 times the length of first. Occipital carina present on the ventral 0.5 of head. Mesosoma: Anterior margin of pronotum broadly truncate, laterally rounded and slightly upcurved. Lateral groove of pronotum weak, not extending past the dorsal 0.3. Pronotum completely glabrous, impunctate. Scutum shiny, impunctate. Epicnemial carina is strongly angled towards the anterior margin of mesopleuron. Mesopleuron with very sparse punctures ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.35 the length of Cu1b. Marginal cell about 2.7 times as long as wide. Propodeum with a posterior vestige of pleural carina present, impunctate. Claws basally pectinate. Metasoma: T1 about 2.3 times as long as broad. Cerci not well developed.

*Male* – none.

*Color* – yellowish to light orange, brownish markings present around ocelli and on the abdominal tergites 2-8. Antennae darkening at tip. Hind femur darker orange to light brownish, rest of leg dark brown. Fore wing hyaline, tip brownish.

*Material Examined* – Holotype: ♀, Braulio Carrillo National Park, 400m, Cartago prov., Costa Rica, 10-11-IV-1985 (Henri Goulet).

*Biological Notes* – host unknown.

*Remarks* – Gauld (1997) has described this species from a single type specimen (see Material Examined section).

***Physotarsus emarginatus* Zhaurova, spec. nov.**

(Figs. 30-32)

*Diagnosis* – lateral ocelli separated by 1.0-1.2 times their widest diameter from each other, and by 1.5-1.7 times their widest diameter from the eye margin. Antenna with 35-38 flagellomeres. Pronotum completely glabrous. Scutum shiny, very sparse punctures present on anterior 0.3. T1 about 2.0 times as long as broad. Head yellow with a black median stripe on frons and vertex. Mesosoma black and yellow (Fig. 28). First tergite of metasoma yellow basally with two black spots on posterior 0.7; rest of tergites largely

dark, some with yellow apical trim. Hind leg entirely orange, terminal tarsi slightly darker than coxa. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 30) 3.9-5.0 mm, fore wing 3.8-5.0 mm. Head (Fig. 31): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 2.6-2.8 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face sparsely covered by very short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.5-0.6 times the width of mandibular base. Face 2.0-2.2 times as broad as long, evenly sparsely punctate, slightly protruding in profile. Interantennal area flat, area immediately behind antennae weakly concave laterally turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of median ocellus about equal widest diameter of torulus. Lateral ocelli separated by 1.0-1.2 times their widest diameter from each other, and by 1.5-1.7 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 35-38 flagellomeres; length of first flagellomere 1.2 times widest transverse diameter of eye; second flagellomere 0.6-0.7 times the length of first. Occipital carina present on the ventral 0.6-0.7 of head. Mesosoma: Anterior margin of the pronotum broadly truncate, laterally rounded and slightly upcurved. Epomia quite strong, extending to the dorsal 0.7, sometimes complete. Pronotum completely glabrous, impunctate. Scutum shiny, very sparse punctures present on the anterior 0.3. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron very sparsely punctate. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.5 times length of Cu1b. Marginal cell about 3.1-3.2 times as long as wide. Propodeum with at least a posterior vestige of pleural carina present, impunctate medially, moderately punctured laterally. Claws basally pectinate. Metasoma: T1 about 2.0 times as long as broad. Cerci not well developed.

*Male* – identical in structure and color to female except subgenital plate with wide deep truncate median incision, its margin even. Aedeagal margin not toothed (Fig. 32).

*Color* – head yellow with a black stripe running down the vertex, originating as low as the apical tooth of the frons. Antennae brown, with a faint stripe of yellow just

before the tip. Occiput black. Mesosoma black and yellow. First tergite of metasoma yellow basally with two black spots on the lower 0.7; rest of tergites largely dark, some with yellow trim; cerci white. Hind leg orange, terminal tarsi slightly darker than base of leg. Fore wing entirely hyaline.

*Material Examined* – 2 females and 2 males. Holotype: ♂, Portal, AZ, USA, 31-VIII-1974, (H&M Townes). Paratypes: 1 ♂, Portal, AZ, USA, 14-VIII-1974, (H&M Townes), 2 ♀, Portal, AZ, USA, 17, 31-VIII-1974, (H&M Townes).

*Biological Notes* – host unknown.

*Remarks* – *emarginatus*: Latin for rounded excavation in male genital plate. Male holotype was designated due to the distinct diagnostic character of this species found in the structure of male subgenital plate.

### ***Physotarsus fabioi* Gauld, 1997**

*Physotarsus fabioi* Gauld, 1997. Yu & Horstmann, 1997: catalog.

This species is removed from *Physotarsus* and from Scolobatini. See discussion, Chapter VI.

### ***Physotarsus flavipennis* Zhaurova, spec. nov.**

(Figs. 33, 34)

*Diagnosis* – lateral ocelli separated by about 1.0 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Antennae yellowish-brown, uniformly darkening towards apex. Pronotum mostly glabrous, sparse punctures present along anterior margin. Scutum shiny, very sparse punctures present on anterior 0.3. T1 about 1.7 times as long as broad. Head yellow with a median black stripe on frons and vertex. Mesosoma with yellow and black spots. Metasoma with T2 largely yellow, other metasomal tergites largely black with yellow apical trim. Hind femur orange, proximal 0.6 of tibia yellow, rest orange, tarsi and pretarsus yellow. Fore wing lightly yellowish with a fuscous tip.

*Description: Female* – body (Fig. 33) 8.6-9.1 mm, fore wing = 6.6-9.0 mm. Head (Fig. 34): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 3.8 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face covered by very short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space about 0.5-0.7 times the width of mandibular base. Face 2.0-2.2 times as broad as long, moderately protruding in profile. Face sparsely punctate laterally, punctures quite strong and dense medially, face may even appear slightly rugose. Interantennal area flat, area immediately behind antennae weakly concave turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus 1.4-1.6 times widest diameter of median ocellus. Lateral ocelli are separated by about 1.0 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 44-47 flagellomeres, length of first flagellomere 1.3-1.4 times widest transverse diameter of eye; second flagellomere 0.6-0.7 times length of first. Occipital carina present on the ventral 0.6-0.7 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally rounded and slightly upcurved. Lateral groove of the pronotum quite strong, extending to about dorsal 0.7, sometimes complete. Pronotum mostly glabrous, impunctate medially, sparsely punctured laterally. Scutum shiny, very sparse punctures present on the anterior 0.3. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleural punctation moderate. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.7 times length of Cu1b. Marginal cell about 3.1-3.2 times as long as wide. Propodeum without carinae, impunctate medially. lateral punctation quite dense. Claws pectinate basally. Metasoma: T1 about 1.7 times as long as broad. Cerci not prominent.

*Male* – subgenital plate with wide, deep, truncate median incision, its margin even. Aedeagal margin not toothed. Structure and color as in female.

*Color* – head yellow with a black stripe running down the vertex, originating as low as the apical tooth of the frons. Antennae darker at the base and tip, gradually becoming lighter in the middle. Occiput black. Mesosoma with yellow and black spots.

Metasoma with T2 largely yellow, other metasomal tergites largely black with yellow trim. Hind femur orange, proximal 0.6 of tibia yellow, rest orange, tarsi and pretarsus yellow. Fore wing largely hyaline with a fuscous tip.

*Material Examined* – 15 females and 9 males. Holotype: ♀, Fredericksburg, TX, USA, 11-V-1988, (H&M Townes). Paratypes: 3 ♀, Fredericksburg, TX, USA, 03,11,17-V-1988, (H&M Townes); 2 ♂, 30-IV- 1988, 17-V-1988, (H&M Townes), 1 ♂, Kerrville, TX, 12-V-1988, (H&M Townes).

*Biological Notes* – host unknown, species from Texas

*Remarks* – *flavus*: Latin for yellow; *pennis*: Latin for wings.

***Physotarsus foveatus* Zhaurova, spec. nov.**

(Figs. 35, 36)

*Diagnosis* – lateral ocelli separated by about 1.8 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Antenna with 29-33 flagellomeres. Pronotum with sparse punctures on anterior and posterior margins, densely punctured to rugose medially. Scutum punctation dense, covering its entire surface. T1 about 2.0 times as long as broad. Head yellow with a wide, black, median stripe originating at the upper half of clypeus and extending to the occiput. Mesosoma almost entirely black with some yellow patterns on the scutum. Metasomal tergites largely black with yellow apical trim; cerci dark. Hind femur orange, tibia and tarsi black. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 35) 4.4-5.9 mm, fore wing 4.5-5 mm. Head (Fig. 36): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 3.2 times as wide as long, not separated medially by a shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate, pointed laterally. Malar space small, about 0.3-0.4 times width of mandibular base. Face 1.9 times as broad as long, quite densely evenly punctate, quite strongly protruding in profile. Interantennal area flat, area immediately behind antennae weakly concave turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.6 of eye height. Interantennal distance about equals distance between



lateral ocelli. Widest diameter of torulus 1.2 times widest diameter of median ocellus. Lateral ocelli separated by about 1.8 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Area between lateral ocelli strongly depressed medially, area immediately behind ocelli not sharply declivitous. Antenna with 29-33 flagellomeres, length of first flagellomere 0.9 times widest transverse diameter of eye, second flagellomere 0.6-0.7 times length of first. Occipital carina present on the ventral 0.7-0.8 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally rounded and slightly upcurved. Lateral groove of the pronotum vestigial, present on the dorsal 0.3. Pronotum with sparse punctures on anterior and posterior margins, densely punctate to rugose medially. Scutum punctation dense, covering its entire surface. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron quite densely punctate with a very small impunctate area. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.75 times length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with pleural carinae complete; propodeum somewhat rugose and impunctate medially with dense punctation laterally. Claws simple. Metasoma: T1 about 2.0 times as long as broad. Cerci not protruding.

*Male* – none

*Color* – head yellow with a wide black stripe originating at the upper half of clypeus and running all across face down to the occiput. Antennae dark basally, gradually becoming lighter towards tip. Mesosoma almost entirely black with some yellow patterns on the scutum. Metasomal tergites largely black with yellow apical trim; cerci dark. Fore and middle legs yellow, apical tarsomeres sometimes dark; hind femur orange, tibia and tarsi black. Fore wing entirely hyaline.

*Material Examined* – I have examined 12 females. Holotype: ♀, Portal, AZ, USA, 18-IX-1987, (H&M Townes); Paratypes: 4 ♀, Portal, AZ, USA, 14,17,28-VIII-1974, and 13-IX-1987, (H&M Townes); 1 ♀, 5mi. S. Monterrey, Nuevo Leon, Mexico, 03-IX-1958, (HF Howden).

*Biological Notes* – host unknown

*Remarks* – *fovea*: Latin for pit, *atus*: l. having the nature of.

***Physotarsus gineus* Zhaurova, spec. nov.**

(Figs. 37, 38)

*Diagnosis* – lateral ocelli separated by about 1.8 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Antenna with 28-29 flagellomeres. Pronotum largely glabrous, sometimes sparsely punctured or slightly rugose medially. Scutum shiny, very sparse punctures present on the anterior 0.3. Mesosoma largely black with sparse yellow markings on the scutum and propodeum. Metasomal segments largely black with a thin apical yellow trim. Hind femur and tibia orange, tarsi brown. Fore wing hyaline, tip fuscous.

*Description: Female* – body (Fig. 37): 3.5-4.1 mm, fore wing 3.6-4.0 mm. Head (Fig. 38): Clypeal margin thick, evenly rounded laterally, with a thick rounded central lobe. Clypeus about 2.9 times as wide as long, not divided medially by a transverse depression, separated from face by a prominent groove. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits extremely elongate and pointed laterally. Malar space small, about 0.3 times width of mandibular base. Face 2.2-2.3 times as broad as long, evenly sparsely punctate, strongly protruding in profile. Interantennal area flat, area immediately behind antennae weakly concave turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.6 of eye height. Interantennal distance smaller than the distance between lateral ocelli. Widest diameter of torulus 1.4-1.6 times widest diameter of median ocellus. Lateral ocelli separated by about 1.8 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 28-29 flagellomeres, length of first flagellomere 0.8 times widest transverse diameter of eye, second flagellomere 0.6-0.7 times length of first. Occipital carina present on the ventral 0.6-0.7 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally rounded and slightly upcurved. Lateral groove of the pronotum weak, present on the dorsal 0.4. Anterior margin of the pronotum straight and slightly upcurved laterally. Pronotum largely glabrous, sometimes sparsely punctured or slightly rugose medially.

Scutum shiny, very sparse punctures present on the anterior 0.3. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron moderately to densely punctate ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.8 times length of Cu1b. Marginal cell about 2.8-2.9 times as long as wide. Propodeum without carinae, impunctate to very lightly punctured medially, quite densely punctate laterally. Claws simple. Metasoma: T1 about 2.3 times as long as broad. Cerci not prominent.

*Male* – subgenital plate with slightly concave even margin. Aedeagal margin not toothed. Structure and color otherwise as in female

*Color* – head pale-yellow, frons and occiput black. Mesosoma largely black with sparse yellow markings on the scutum and propodeum. Metasomal segments largely black with a thin yellow trim; cerci dark. Fore and middle legs yellow, hind femur and tibia orange, tarsi brown. Fore wing hyaline, tip fuscous.

*Material Examined* – 4 females and 5 males. Holotype: ♀, nr. Roosevelt L. AZ, USA, 27-IV-1947, (H&M Townes); Paratypes: 1 ♀, Maricopa mtns, AZ, USA, 13-IV-1947, (H&M Townes); 2 ♀, nr. Roosevelt L. AZ, USA, 21-IV-1947, (H&M Townes); 1 ♂, Maricopa mtns, AZ, USA, 13-IV-1947, (H&M Townes); 1 ♂, nr. Roosevelt L. AZ, USA, 29-IV-1947, (H&M Townes); 1 ♂, Ajo, AZ, USA, 09-IV-1947, (H&M Townes); 1 ♂, Sinton, TX, USA, VI-1975, (V Nealis); 1 ♂, 22 mi. W. Seminole, Gaines co., TX, USA, 25-IV-1971, (CR Ward) on Mesquite

*Biological Notes* – host unknown. One specimen found on Mesquite.

***Physotarsus glabellus* Zhaurova, spec. nov.**

(Figs. 39, 40)

*Diagnosis* – lateral ocelli separated by 0.4 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Antenna with 22-23 flagellomeres. Pronotum and scutum shiny, impunctate. T1 about 1.5 times as long as broad, spiracles protruding in profile. Clypeus light yellowish to white, face yellow, frons mostly yellow to entirely brown. Mesosoma entirely orange. Metasoma with T1 entirely brown, rest of tergites mostly brown with yellow apical trim; sternites brownish-

yellow. Fore and middle legs yellow, most of hind femur and tibia yellow, with the extreme apices brownish; tarsi dark brown to black. Cerci light-brown. Fore wing hyaline with dusky apex.

*Description: Female* – body (Fig. 39) 3.7-4.0 mm, fore wing 3.7 mm. Head (Fig. 40): Clypeal margin widely rounded laterally, with a thick somewhat angulate central lobe. Clypeus about 2.7 times as wide as long, divided medially by a shallow transverse depression. Clypeus, mandibles and face sparsely covered by moderately long setae. Anterior tentorial pits oval. Malar space 0.5-0.6 times width of mandibular base. Face about 1.5 times as broad as long, smooth. Interantennal area flat, area immediately behind antenna weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus about 1.2 times widest diameter of median ocellus. Lateral ocelli separated by 0.4 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli sharply declivitous. Antenna with 22-23 flagellomeres, length of first flagellomere about equals widest transverse diameter of eye; second flagellomere about 0.7 times length of first. Occipital carina present on the ventral 0.4 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally truncate, upcurved. Lateral groove of the pronotum present on the dorsal 0.3. Pronotum concave medially. Pronotum and scutum glabrous, shiny, impunctate. Epicnemial carina is strongly angled towards the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent on the ventral half. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 times length of Cu1b. Marginal cell about 2.8 times as long as wide. Propodeum with posterior vestiges of median longitudinal carina, pleural carina absent, impunctate medially, sparsely pubescent laterally. Claws basally pectinate. Metasoma: T1 about 1.5 times as long as broad, spiracles protruding in profile. Cerci not protruding.

*Male* – none

*Color* – clypeus white, face yellow, frons mostly yellow to entirely brown. Antennae light brown at base, becoming darker towards apex. Mesosoma entirely orange. Metasoma with T1 entirely brown, rest of tergites mostly brown with yellow apical trim; sternites brownish-yellow. Fore and middle legs yellow, most of hind femur and tibia

yellow, with the extreme apices brownish; tarsi dark brown to black. Cerci light-brown. Fore wing hyaline with dusky apex.

*Material Examined* – 2 females. Holotype ♀, Caruaru, 900m, Brazil, IV-1972, (M Alvarenga); Paratype: ♀, same label as holotype.

*Biological Notes* – host unknown, species alpine, found at altitude of 900m.

*Remarks* – *glaber*: Latin for hairless, smooth; *ellus*: Latin for diminutive, small.

***Physotarsus laucos* Zhaurova, spec. nov.**

(Figs. 41, 42)

*Diagnosis* – lateral ocelli separated by 0.9-1.0 times their widest diameter from each other, and by about 1.7 times their widest diameter from the eye margin. Antenna with 24 flagellomeres. Pronotum and scutum shiny, impunctate. T1 about 2.0 times as long as broad, spiracles protruding in profile. Head and mesosoma entirely yellowish-brown. Metasomal tergites brown with thin white apical trim, sternites white. Hind leg brown. Fore wing hyaline with dusky apex.

*Description: Female* – body (Fig. 41) 4.4-4.6 mm, fore wing 4.6-4.8 mm. *Head* (Fig. 42): Clypeal margin widely rounded laterally, with a thick somewhat angulate central lobe. Clypeus about 2.6 times as wide as long, not divided medially by a transverse depression. Clypeus, mandibles and face sparsely covered by moderately long setae. Anterior tentorial pits oval. Malar space 0.5-0.6 times width of mandibular base. Face about 1.5 times as broad as long, smooth. Interantennal area slightly concave, area immediately behind antenna weakly concave, turning convex laterally before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus about 1.2 times widest diameter of median ocellus. Lateral ocelli separated by 0.9-1.0 times their widest diameter from each other, and by about 1.7 times their widest diameter from the eye margin. Area between lateral ocelli flat to slightly depressed, area behind ocelli sharply declivitous. Antenna with 24 flagellomeres, length of first flagellomere about equal widest diameter of eye; second flagellomere about 0.7 times length of first. Occipital carina present on the ventral 0.4 of head. Mesosoma: Anterior margin of the

pronotum medially emarginate, laterally truncate, upcurved. Lateral groove of the pronotum present on the dorsal 0.3. Pronotum and scutum shiny, impunctate. Epicnemial carina is strongly angled towards the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent on the ventral half. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 times length of Cu1b. Marginal cell about 2.6 times as long as wide. Propodeum with complete pleural carinae, impunctate medially, sparsely pubescent laterally. Claws basally pectinate. Metasoma: T1 about 2.2 times as long as broad, spiracles protruding in profile. Cerci protruding. Female subgenital plate widely rounded, larger than usual.

*Male* – none

*Color* – head and mesosoma entirely orange. Antennae yellow to light-brown. Metasomal tergites brown with thin white trim, sternites white. Subgenital plate white with thin brown apical margin. Cerci light-brown. Fore and middle legs orange with dark apex; hind leg brown. Fore wing hyaline with dusky apex.

*Material Examined* – 2 females. Holotype: ♀, S.J. Barreiro, Serra de Bocaina, 1650m, Brazil, XI-1968, (Alvarenga & Seabra). Paratype: ♀, Caruaru, 900m, Brazil, VI-1972, (J. Lima).

*Biological Notes* – host unknown, species found in highlands at altitudes of 900-1650m.

*Remarks* – *laucos* is Greek for white.

***Physotarsus luteus* Zhaurova, spec. nov.**

(Figs. 43, 44)

*Diagnosis* – lateral ocelli separated by 1.0 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Antenna with 28 flagellomeres. Pronotum completely glabrous, shiny. Scutum shiny, very sparse punctures present on the anterior 0.3. T1 about 2.0 times as long as broad. Head yellow, face mostly yellow, sometimes light brownish medially. Mesosoma entirely yellow. Metasoma with first tergite yellow, rest of tergites mostly light orange with yellow apical

trim. Hind femur and tibia yellow to light-orange, tarsi dark brown to black. Fore wing hyaline.

*Description: Female* – body (Fig. 43) 3.7-4.2 mm, fore wing 3.5-4.0 mm. Head (Fig. 44): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 2.7 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.6 times width of mandibular base. Face 1.7 times as broad as long, quite flat, terminating dorsally with a median tooth. Face evenly sparsely punctured. Interantennal area flat, area immediately behind toruli weakly concave, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus 1.5 times widest diameter of median ocellus. Lateral ocelli separated by 1.0 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli sharply declivitous. Antenna with 28 flagellomeres, length of first flagellomere 1.2 times widest transverse diameter of eye, second flagellomere 0.7 times length of first. Occipital carina present on the ventral 0.3 of head. Mesosoma: Anterior margin of the pronotum medially slightly emarginate, laterally rounded and upcurved. Lateral groove of the pronotum present on the dorsal 0.5. Pronotum glabrous, impunctate, shiny. Scutum shiny, very sparse punctures present on the anterior 0.3. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.7 times length of Cu1b. Marginal cell about 3.3 times as long as wide. Propodeum without carinae, impunctate medially, sparsely pubescent laterally. Claws basally pectinate. Metasoma: T1 about 2.0 times as long as broad, spiracles not protruding in profile; cerci not protruding.

*Male* – none

*Color* – head yellow, face mostly yellow, sometimes light-brownish medially. Antennae yellow, becoming dark at the tip. Mesosoma entirely yellow. Metasoma with first tergite yellow, rest of tergites mostly light-orange with yellow trim. Fore and middle

legs yellow; hind femur and tibia yellow to light-orange, tarsi dark brown to black. Fore wing hyaline.

*Material Examined* – 2 females. Holotype: ♀, Yucatan Merida, Xmatkuil, 25-V-1996, (R Wharton); Paratype: ♀, Estacion Biologica Chamela Trampa, Jalisco, Mexico, 4-5-VII-1993, (R. Wharton & M. Sharkey), Malaise trap.

*Biological notes* – host unknown, paratype caught in malaise trap.

*Remarks* – *luteus* is Latin for yellow.

***Physotarsus maculipennis* (Cresson, 1874)**

(Figs. 45, 46)

*Tryphon maculipennis* Cresson, 1874. Syntype ♂ in BMNH. Dalla Torre (1902): catalog. Cresson (1916): The Cresson types of Hymenoptera. Townes (1946): type checklist.

*Physotarsus maculipennis*: Townes and Townes (1966): description of genus with designation of *P. maculipennis* as the type species. Townes (1970 b): copy of original generic description, listing the type species. Yu and Horstmann (1997): catalog, p. 455.

*Diagnosis* – lateral ocelli separated by 0.9 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Antenna with 37 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 2.2-2.4 times as long as broad, spiracles somewhat protruding in profile. Head entirely reddish-brown. Mesosoma mostly reddish-brown, sometimes with black markings laterally. Metasoma largely reddish-brown. Hind leg orange, tarsi 2 and 3 white. Fore wing blackish, with two pale yellowish bands on either side of stigma (Fig. 43).

*Description: Female* – Body (Fig. 45) 8.3-9.7 mm, fore wing 9.0-9.2 mm. Head (Fig. 46): Clypeal margin widely truncate laterally, with a thick, somewhat angulate central lobe. Clypeus about 3.0 times as wide as long, divided medially by a transverse depression, with two small basolateral lobes weakly protruding in profile. Clypeus, mandibles and face densely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.5-0.6 times width of mandibular base. Face 1.8 times as broad as long, quite prominently protruding in profile; face punctures quite dense, not



very deep. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus 1.4 times widest diameter of median ocellus. Lateral ocelli separated by 0.9 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli not sharply declivitous. Antenna with 37 flagellomeres; length of first flagellomere 1.4 times widest transverse diameter of eye, second flagellomere 0.6 times the length of first. Occipital carina present on the ventral 0.2-0.3 of head. Mesosoma: Anterior margin of the pronotum medially slightly emarginate, laterally rounded, slightly upcurved. Lateral groove of the pronotum present on the dorsal 0.3. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.8-0.9 times length of Cu1b. Marginal cell about 2.5-3.1 times as long as wide. Propodeum with pleural carina almost entirely complete, interrupted medially. Propodeum impunctate medially, quite densely punctate laterally. Claws almost fully pectinate. Metasoma: T1 about 2.2-2.4 times as long as broad, spiracles somewhat protruding in profile. Cerci not protruding.

*Male* – subgenital plate with margin not emarginate, widely truncate. Aedeagal margin not toothed. Structure and color otherwise as in female.

*Color* – head and antennae entirely reddish-brown. Mesosoma mostly reddish-brown, sometimes with black markings laterally. Black pigment is also sometimes present on the tip of antennae and dorsally on the metasoma. Metasoma largely reddish-brown, T1 black basally around glymma. Anterior two pairs of legs entirely reddish-brown, hind leg reddish-brown, tarsi 2 and 3 white. Fore wing blackish, with two pale yellowish bands on fore wing; pterostigma dark.

*Material Examined* – 4 females and 2 males. 1 ♀, Chapala, Jalisco, Mexico, X-15-1968, (C. E. Bohart); 1 ♀, Guandalajara, Jalisco, Mexico, 16-VII-1951, (HE Evans); 1 ♀, San Luis Potosi, El Salto, Mexico, 21-VII-1962; 1 ♀, 6mi E. Xilitla, 2000ft, Mexico, 31-VII-1962 (RH&EM Painter). 1 ♂, Xilitla, S.L.P, Mexico, 30-VII-1962, (RH&EM Painter); 1 ♂, Guadalajara, Mexico, 23-VII-1939, (CH Townes).

*Biological Notes* – host unknown, species found at altitude of 610 m

***Physotarsus melipennis* Zhaurova, spec. nov.**

(Figs. 47, 48)

*Diagnosis* – lateral ocelli separated by about 1.6 times their widest diameter from each other, and by about 2.8 times their widest diameter from the eye margin. Antenna with 33-36 flagellomeres. Pronotum sparsely to moderately punctate. Scutum shiny, sparsely punctate on the anterior 0.4. T1 about 2.0 times as long as broad. Head, mesosoma and metasoma entirely orange. Antennae black. Fore and middle legs orange; hind femur and tibia orange, tarsi black. Fore wing entirely fuscous.

*Description: Female* – body (Fig. 47) 5.0-6.8 mm, fore wing 4.6-5.5 mm. Head (Fig. 48): Clypeal margin widely rounded laterally with a thick rounded central lobe; Clypeus about 2.0 as wide as long, anterior part somewhat impressed. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate, pointed laterally. Malar space about 0.4 times width of mandibular base. Face about 2.0 times as broad as long, evenly punctured, slightly raised medially. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance about 1.2 times the distance between lateral ocelli. Widest diameter of torulus about 1.4 times widest diameter of median ocellus. Lateral ocelli separated by about 1.6 times their widest diameter from each other, and by about 2.8 times their widest diameter from the eye margin. Area between lateral ocelli strongly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 33-36 flagellomeres, length of first flagellomere 1.3 times widest transverse diameter of eye, second flagellomere about 0.6-0.7 times length of first. Occipital carina present on the ventral 0.5 of head. Mesosoma: Anterior margin of the pronotum broadly truncate, flat medially, slightly upcurved laterally. Lateral groove of the pronotum present on the dorsal 0.4. Pronotum sparsely to moderately punctate. Scutum shiny, sparsely punctate on the anterior 0.4. Epicnemial carina parallels the anterior margin of mesopleuron.

Mesopleuron quite densely punctured, with a very small impunctate area. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 1.0 the length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with pleural carinae vestigial to complete, narrowly impunctate posteromedially, densely punctate laterally. Claws simple. Metasoma: T1 about 2.0 times as long as broad, spiracles not raised in profile. Cerci protruding.

*Male* – none

*Color* – head, mesosoma and metasoma entirely orange. Antennae black. Fore and middle legs orange; hind femur and tibia orange, tarsi black. Fore wing entirely fuscous.

*Material Examined* – 5 females. Holotype: ♀, Portal, AZ, USA, 17-VIII-1974, (H&M Townes); Paratypes: 4 ♀, Portal, AZ, USA, 13, 14, 17, 30-VIII-1974, (H&M Townes).

*Biological Notes* – host unknown.

*Remarks* – *melas* is Greek for dark or black, *pennis* is Latin for wing. One specimen was found to exhibit an occipital groove dorsally invaginated at vertex. It is discounted to mutation as no other Scolobatini taxa have a complete occipital carina.

***Physotarsus melotarsus* Zhaurova, spec. nov.**

(Figs. 49, 50)

*Diagnosis* – lateral ocelli separated by 1.8 times their widest diameter from each other, and by 1.7 times their widest diameter from the eye margin. Antenna with 27-28 flagellomeres. Pronotum impunctate, rugose medially and along basal margin. Scutum punctation dense, covering its entire surface. T1 about 1.5-1.6 times as long as broad. Face yellow, frons medially and occiput black. Mesosoma black and yellow (Fig. 47). Metasomal tergites mostly black with apical yellow margins. Hind femur and tibia orange, tarsi and pretarsus black. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 49) 4.0-4.5 mm, fore wing 3.6-3.8 mm. Head (Fig. 50): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 2.6 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face covered by sparse short setae. Anterior tentorial

pits elongate and upcurved laterally. Malar space 0.2-0.3 times width of mandibular base. Face about 2.2 times as broad as long, quite strongly protruding in profile; punctation quite dense, slightly more so medially. Interantennal area flat, area immediately behind antennae weakly concave laterally turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance about equal distance between lateral ocelli. Widest diameter of torulus 1.3 times widest diameter of median ocellus. Lateral ocelli separated by 1.8 times their widest diameter from each other, and by 1.7 times their widest diameter from the eye margin. Area between lateral ocelli quite strongly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 27-28 flagellomeres, length of first flagellomere 0.8 times the widest transverse diameter of eye; second flagellomere 0.8 times length of first. Occipital carina present on the ventral 0.7 of head. Mesosoma: Anterior margin of the pronotum medially very slightly emarginate, laterally rounded and slightly upcurved. Lateral groove of the pronotum complete, widely rugose laterally. Pronotum impunctate, rugose medially and along posterior margin. Scutum punctation dense, covering its entire surface. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron quite densely punctate, impunctate area small. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.5 times length of Cu1b. Marginal cell about 2.8-2.9 times as long as wide. Propodeum with posterior vestiges of pleural carinae, or without carinae entirely, narrowly impunctate posteromedially, densely punctate laterally. Claws basally pectinate. Metasoma: T1 about 1.6-1.8 times as long as broad. Cerci protruding.

*Male* – antennae with 30 flagellomeres. Structure and color are otherwise as in female.

*Color* – frons and occiput black. Antennae orange to brownish. Mesosoma black and yellow. Metasomal tergites mostly black with thin apical yellow margins. Fore and middle legs yellow, apical tarsomeres sometimes dark; hind femur and tibia orange, tarsi and pretarsus black. Fore wing entirely hyaline.

*Material Examined* – 5 females and 1 male. Holotype: ♀, Casa Blanca Intern. State Park, Laredo, TX, USA. 08-III-2001. At light, after 11:00 PM (W.F. Chamberlain). Paratypes: sex unknown – abdomen missing, Overton NV. 12-V-1930 (E.W. Davis) *Prosopsis glandulosa* (honey mesquite); ♀, Fredericksburg, TX, USA, 05-07-V-1998

(H&M Townes), ♀, 8 miles S.W. of Port Mansfield, TX, USA, 18-III-1994 (W.F. Chamberlain); ♀, San Ygnacio, TX, USA, 18-III-1994, (W. F. Chamberlain), at light; ♀, Sutton Co., 16 mi. W. Sonora, TX, USA, 11-V-1997, (Gillogly & Schaffner); ♂, Crockett Co., 16.7 mi. W. Ozona, TX, USA, 09-V-1997, (Gillogly & Schaffner).

*Biological Notes* – host unknown, holotype collected at light after 11:00 PM, possibly nocturnal. One ♀ specimen from Andreas Canyon, Palm Springs, CA, USA, 31-III-1955, (WRM Mason) (CNC) is very similar to *P. melipennis*, with hind tarsi orange to light brown.

*Remarks* – *melas* is Greek for black; *tarsus* is Greek for tarsal segment.

***Physotarsus montezuma* (Cameron, 1886)**

*Mesoleius montezuma* Cameron, 1886: species description and color plate.

*Scopesis flavolineatus* Cameron, 1904, synonymized by Townes and Townes (1966), who noted that the two species had the same type specimen.

*Physotarsus montezuma*: Townes and Townes (1966): transfer to *Physotarsus*. Yu and Horstmann (1997): catalog, p. 455.

*Description from (Cameron, 1886)* – “Shining, impunctate, covered with a short, sparse pile. Antennae long, slender, nearly one fourth longer than body. The mouth, the mandibles (except at the apices, which are piceous), the inner orbits of the eyes broadly, a large mark in the centre of the face, the tegulae, the scutellum, the postscutellum, the four anterior legs (except the bases of the coxae and the tips of the tarsal joints), the greater part of the hind femora and tibiae beneath, the tibial spurs at the base, the basal segments of the abdomen broadly, the other segments narrowly at the base, and the ventral surface, yellow, tinged slightly with fulvous. Hind legs longish (the tarsi considerably longer than the tibiae), rather stout, the apical part of the claw bare. Head a little broader than the mesothorax; eyes large; the face not bucculate, the clypeus slightly and broadly incised. Scutellum slightly convex. Metathorax without keels, having a gradual slope; the sides slightly aciculated and pilose. Abdomen not much longer than the head and thorax together, becoming gradually thicker toward the apex; petiole narrowed at the base,

becoming gradually wider towards the apex. Wings are a little shorter than the body, without an areolet.”

*Remarks* – Townes has recorded 1 ♂ type specimen: Mexico: Ciudad in Durango at 8,100 ft (2,469 m). It is important to note that the description mentions the lack of areolet in the wing, the tarsi being considerably longer than the tibia, and the original plate clearly demonstrates the lack of the abscissa of 1A vein in the hind wing.

***Physotarsus niveus* Zhaurova, spec. nov.**

(Figs. 51, 52)

*Diagnosis* – lateral ocelli separated by about 0.6 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Antenna with 24-27 flagellomeres. Pronotum and scutum shiny, impunctate. T1 about 2.2 times as long as broad, spiracles protruding in profile. Anterior margin of clypeus white, rest of clypeus, head and mesosoma orange. Anterior median 0.6 of propodeum brown, rest white. Metasoma with T1 white anteriorly, brown posteriorly; rest of tergites brown with thin white apical margins, sternites white. Hind leg dark brown to black, inner lateral sides of femur and tibia white. Fore wing hyaline.

*Description: Female* – body (Fig. 51) 5.2-5.8 mm, fore wing 5.5 mm. Head (Fig. 52): Clypeal margin widely rounded laterally, with a thick somewhat angulate central lobe. Clypeus about 2.8 times as wide as long, not divided medially by a transverse depression. Clypeus, mandibles and face sparsely covered by moderately long setae. Anterior tentorial pits oval. Malar space about 0.5 times width of mandibular base. Face about 1.5-1.6 times as broad as long, smooth. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.8 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus about equal widest diameter of median ocellus. Lateral ocelli separated by about 0.6 times their widest diameter from each other, and by about 2.0 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area behind ocelli sharply declivitous. Antenna with 24-27 flagellomeres, length of first flagellomere 0.9 times

widest transverse diameter of eye; second flagellomere about 0.7 times length of first. Occipital carina present on the ventral 0.2 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally truncate and slightly upcurved. Lateral groove of the pronotum present on the dorsal 0.2. Pronotum and scutum shiny, impunctate. Epicnemial carina is strongly angled towards the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 the length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with posterior vestiges of median longitudinal and pleural carinae distinct. Impunctate medially, sparsely pubescent laterally. Claws basally pectinate. Metasoma: T1 about 2.2 times as long as broad, spiracles protruding in profile. Cerci protruding.

*Male* – body 4.8mm, genital plate small, transparent, weakly sclerotized.

Structure and color otherwise as in female.

*Color* – anterior margin of clypeus white, rest of clypeus, head and mesosoma orange. Antennae dark. Anterior median 0.6 of propodeum brown, rest white. Metasoma with T1 white anteriorly, brown posteriorly; rest of tergites brown with thin white apical margins, sternites white. Fore and middle legs orange with dark apex; hind leg dark brown to black, inner lateral sides of femur and tibia white. Cerci brown. Fore wing hyaline.

*Material Examined* – 2 females and 1 male. Holotype: ♀, S.J. Barriero, Serra da Bocaina, 1650m, Brazil, XI-1968, (Alvarenga & Seabra); Paratypes: 1 ♀, S.J. Barriero, Serra da Bocaina, S.P. XI-1969, (Alvarenga & Seabra); 1 ♂, Floresta da Tijuca, Guan., Brazil, IV-1969, (Alvarenga & Seabra).

*Biological Notes* – host unknown, species found in highlands at 1650m.

*Remarks* – *niveus* is Latin for white.

***Physotarsus oculatus* Zhaurova, spec. nov.**

(Figs. 53, 54)

*Diagnosis* – lateral ocelli separated by about 0.8 times their widest diameter from each other, and by about 1.5 times their widest diameter from the eye margin. Antenna

with 27 flagellomeres. Pronotum and scutum impunctate, shiny. T1 about 2.2 times as long as broad, spiracles protruding in profile. Face white or very light yellow; ocellar area dark-brown, lateral frons and occiput orange. Mesosoma with anterior part of the pronotum brown; posterior part white; scutum and scutellum orange; mesopleuron white; propodeum white with two anterior lateral brown spots. Metasomal tergites brown with apical white margins, sternites white. Hind legs entirely black. Fore wing hyaline with dusky apex.

*Description: Female* – body (Fig. 53) 4.4-4.7 mm, fore wing 4.0-4.3 mm. Head (Fig. 54): Clypeal margin widely truncate laterally with a thick, somewhat angulate central lobe. Clypeus about 3.4 times as wide as long, separated medially by a shallow transverse depression; Clypeus, mandibles and face sparsely covered by moderately long setae. Anterior tentorial pits elongate, pointed laterally. Malar space about 0.5 times width of mandibular base. Face about 1.4 times as broad as long, sparsely evenly punctured. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus about equal widest diameter of median ocellus. Lateral ocelli separated by about 0.8 times their widest diameter from each other, and by about 1.5 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed, area immediately behind ocelli sharply declivitous. Antenna with 27 flagellomeres, length of first flagellomere about 0.7 times widest diameter of eye; second flagellomere about 0.7 times the length of first. Occipital carina present on the ventral 0.4 of head. Mesosoma: Anterior margin of the pronotum quite strongly emarginate medially, laterally truncate and slightly upcurved. Lateral groove of the pronotum present on the dorsal 0.4. Pronotum and scutum glabrous, impunctate, shiny. Epicnemial carina strongly downturned towards the anterior margin of mesopleuron. Mesopleuron shiny, very sparsely punctured on ventral 0.7. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.4 times length of Cu1b. Marginal cell about 2.9 times as long as wide. Propodeum with a posterior vestige of pleural carinae, impunctate medially, sparsely pubescent laterally. Claws basally pectinate. Metasoma: T1 about 2.2 times as long as



broad, spiracles protruding in profile. Subgenital plate widely rounded, larger than usual. Cerci not protruding.

*Male* – none

*Color* – face white or very light yellow; ocellar area dark-brown, lateral frons and occiput orange. Antenna uniformly yellowish. Mesosoma with anterior part of the pronotum brown; posterior part white; scutum and scutellum orange; mesopleuron white; propodeum white with two lateral brown spots. Metasomal tergites brown with white margins, sternites white. Genital plate white with thin brown apical margin. Cerci brown. Fore legs yellow, middle legs yellow with black tarsi; hind legs entirely black. Fore wing hyaline with dusky apex.

*Material Examined* – 2 females. Holotype: ♀, Jacareacanga, Para, Brazil, XII-1968, (M Alvarenga); Paratype: ♀, same label data as holotype.

*Biological Notes* – host unknown.

*Remarks* – *ocules*: Latin for compound eye.

***Physotarsus tonicus* Zhaurova, spec. nov.**

(Figs 55-57)

*Diagnosis* – lateral ocelli are separated by about 1.6 times their widest diameter from each other, and by about 1.4 times their widest diameter from the eye margin. Antenna with 27-31 flagellomeres. Pronotum impunctate, rugose medially and along basal margin. Scutum punctation dense, irregular. T1 about 2.0 times as long as broad. Head yellow and black, females with a thick median longitudinal black stripe on yellow face, males with face entirely yellow. Mesosoma almost entirely black, some yellow pigment sometimes present laterally on the scutum and propodeum. Metasomal tergites mostly black with narrow, white apical trim. Hind femur and tibia orange, coxae, trochanters, tarsi and pretarsi black. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 55) 3.7-4.8 mm, fore wing 3.2-4.0 mm. Head (Fig. 56): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 2.8-3.0 times as wide as long, divided medially by a very shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae.

Anterior tentorial pits elongate, pointed laterally. Malar space small, about 0.25-0.35 times width of mandibular base. Face 1.7-1.8 times as broad as long, quite densely evenly punctate, quite strongly protruding in profile. Interantennal area flat, area immediately behind antenna weakly concave turning convex laterally before reaching ocelli. Anterior margin of torulus situated at about 0.6 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus about 1.4 times widest diameter of median ocellus. Lateral ocelli are separated by about 1.6 times their widest diameter from each other, and by about 1.4 times their widest diameter from the eye margin. Area between lateral ocelli strongly depressed, area immediately behind ocelli not sharply declivitous. Antenna with 27-31 flagellomeres, length of first flagellomere 0.8 times widest transverse diameter of eye, second flagellomere 0.7-0.8 times length of first. Occipital carina present on the ventral 0.7-0.8 of head. Mesosoma: Anterior margin of the pronotum medially emarginate, laterally rounded, slightly upcurved. Lateral groove of the pronotum strong, complete, widely rugose laterally. Pronotum impunctate, rugose medially and along anterior margin. Scutum punctation dense, irregular. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron with a prominent impunctate area. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.75 times length of Cu1b. Marginal cell about 3.0 times as long as wide. Propodeum with pleural carinae vestigial to complete, narrowly impunctate posteromedially, densely punctate laterally. Claws basally pectinate. Metasoma: T1 about 2.0 times as long as broad. Cerci protruding.

*Male* – sexually dimorphic in face color: male face all yellow, lacking the fuscous to black stripe across face (Fig. 57). Subgenital plate elongate, its margin widely truncate, even, aedeagal margin not toothed.

*Color* – face yellow with a thick median longitudinal black, occiput black. Antennae black basally to brownish apically. Mesosoma almost entirely black, some yellow pigment sometimes present laterally on the scutum and propodeum. Metasomal tergites mostly black with white apical trim. Fore and middle legs black basally, yellow apically; hind femur and tibia orange, tarsi and pretarsus black. Fore wing entirely hyaline.

*Material Examined* – 20 females and 41 males. Holotype: ♀, Portal, AZ, USA, 12-IX-1987, (H&M Townes); Paratypes: 1 ♀, nr Roosevelt L, AZ, USA, 29-IV-1947, (H&M Townes); 5 ♀, Portal, AZ, USA, 13,20-VIII-1987, 04,12,21-IX-1987, (H&M Townes); 4 ♂, Portal, AZ, USA, 12,23-VIII-1974, 12,21,-IX-1987, (H&M Townes).

*Biological Notes* – host unknown. Sexual dimorphism in face color observed in this species is a unique and the only such occurrence in species of *Physotarsus*.

***Physotarsus truncatus* Zhaurova, spec. nov.**

(Figs. 58-61)

*Diagnosis* – lateral ocelli separated by 1.2-1.5 times their widest diameter from each other, and by about twice their widest diameter from the eye margin. Antenna with 36-38 flagellomeres. Pronotum glabrous medially around and below the epomia, punctate anterolaterally. Scutum shiny, very sparsely punctured on the anterior 0.4. T1 about 1.7-1.9 times as long as broad. Head yellow with a black stripe running down the vertex. Mesosoma largely black dorsally and laterally with a small yellow spot on the scutum medially (Fig. 61). T1 yellow basally with two black spots on the posterolateral 0.7; rest of metasoma orange. Hind femur, tibia, tarsi and pretarsus uniformly orange. Fore wing entirely hyaline.

*Description: Female* – body (Fig. 58) 4.8-6.0 mm, fore wing 4.5-4.8 mm. Head (Fig. 59): Clypeal margin widely subtruncate laterally, with a thick rounded central lobe. Clypeus about 2.4 times as wide as long, divided medially by a shallow transverse depression. Clypeus, mandibles and face sparsely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.5-0.6 times width of mandibular base. Face twice as broad as long, slightly protruding in profile, terminating dorsally with a median tooth; face punctures not very dense laterally, denser medially. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus 1.4-1.6 times widest diameter of median ocellus. Lateral ocelli separated by 1.2-1.5 times their widest diameter from each other, and by about twice their

widest diameter from the eye margin. Area between lateral ocelli slightly depressed; area immediately behind ocelli not sharply declivitous. Antenna with 36-38 flagellomeres; length of first flagellomere 1.3 times widest transverse diameter of eye, second flagellomere 0.4-0.5 times length of first. Occipital carina present on the ventral 0.6-0.7 of head. *Mesosoma*: Anterior margin of the pronotum medially slightly emarginate, laterally rounded and upcurved. Lateral groove of the pronotum quite strong, present on the dorsal 0.6. Pronotum glabrous medially around and below the epomia, punctate anterolaterally. Scutum shiny, very sparsely punctured on the anterior 0.4 (Fig. 61). Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron quite densely punctate ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.6 times length of Cu1b. Marginal cell about 3.1-3.2 times as long as wide. Propodeum without carinae, impunctate and glabrous medially, moderate punctures and pubescence present laterally. Claws simple. Metasoma: T1 about 1.7-1.9 times as long as broad; spiracles not protruding, cerci protruding.

*Male* – subgenital plate (Fig. 60) with wide, deep, truncate median incision, its margin even. Aedeagal margin not toothed. Structure and color otherwise similar to females.

*Color* – head yellow with a black stripe running down the vertex, originating as low as the apical tooth of the frons. Antennae darker at the base and tip, gradually becoming lighter in the middle. Occiput black. Mesosoma largely black dorsally with a small yellow spot on the scutum medially (Fig. 61). First tergite of the metasoma yellow basally with two black spots on the lower lateral 0.7; rest of metasoma orange. Hind femur, tibia, tarsi and pretarsus uniformly orange. cerci dark. Fore wing entirely hyaline.

*Material Examined* – 10 females and 1 male. Holotype: ♂, Fredericksburg, TX, USA, 07-V-1988, (H&M Townes); Paratypes: 5 ♀, Fredericksburg, TX, USA, 30-IV-1988, 09,13,15,19-V-1988, (H&M Townes).

*Biological Notes* – host unknown.

*Remarks* – *truncatus* is Latin for truncate, after a truncate excavation in male genital plate.

***Physotarsus varicornis* (Cameron, 1886)**

(Figs. 62,63)

*Scolobates varicornis* Cameron, 1886. Syntype ♂ in BMNH.

*Scolobates varicornis* Dalla Torre, 1901. Townes (1966): unjustified emendation.

*Physotarsus davidi* Gauld, 1997. Holotype in AEI, new synonym. Yu & Horstmann, 1997: catalog, p. 455.

*Diagnosis* – lateral ocelli separated by 0.8 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Antenna with 35-38 flagellomeres. Pronotum and scutum glabrous, impunctate. T1 about 1.9-2.1 times as long as broad, spiracles somewhat protruding in profile. Head entirely reddish brown. Mesosoma black with upper part of pronotum, anterior part of mesoscutum and upper margin of mesopleuron reddish brown. Metasoma black with sternites paler yellowish brown. Hind legs black, trochantellus reddish, distal 0.5 of basitarsus and remaining tarsomeres bright yellow. Fore wing blackish with a subapical pale yellowish band.

*Description: Female* – body (Fig. 62) 7.4-8.9 mm, fore wing 7.0-9.5 mm. Head (Fig. 63): Clypeal margin widely truncate laterally, with a thick, somewhat angulate central lobe. Clypeus about 2.8 times as wide as long, divided medially by a transverse depression, with two small basolateral lobes weakly protruding in profile. Clypeus, mandibles and face quite densely covered by short setae. Anterior tentorial pits elongate and upcurved laterally. Malar space 0.5-0.6 times width of mandibular base. Face 1.8 times as broad as long, slightly protruding in profile; punctures quite dense, not very deep. Interantennal area flat, area immediately behind antennae weakly concave laterally, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.7 of eye height. Interantennal distance greater than distance between lateral ocelli. Widest diameter of torulus 1.4 times widest diameter of median ocellus. Lateral ocelli separated by 0.8 times their widest diameter from each other, and by about 1.8-2.0 times their widest diameter from the eye margin. Area between lateral ocelli flat, area behind ocelli not sharply declivitous. Antenna with 35-38 flagellomeres; length of first flagellomere

1.2 times widest transverse diameter of eye, second flagellomere 0.6 times the length of first. Occipital carina present on the ventral 0.2-0.3 of head. Mesosoma: Anterior margin of pronotum medially slightly bifurcate, laterally rounded, slightly upcurved. Lateral groove of pronotum vestigial, present on dorsal 0.2. Pronotum and scutum glabrous, impunctate. Epicnemial carina parallels the anterior margin of mesopleuron. Mesopleuron impunctate, sparsely pubescent ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.8-0.9 the length of Cu1b. Marginal cell about 2.5-3.1 times as long as wide. Propodeum with pleural carina almost entirely complete, interrupted medially, impunctate medially, quite densely pubescent laterally. Claws almost fully pectinate. Metasoma: T1 about 1.9-2.1 times as long as broad, spiracles somewhat protruding in profile. Cerci not protruding.

*Male* – similar to female structure and color.

*Color* – head uniformly reddish brown antenna with scape and pedicel reddish brown, flagellum blackish brown, becoming black, but with a rather ill defined subapical dirty whitish band. Mesosoma black with upper part of pronotum, anterior part of mesoscutum and upper margin of mesopleuron reddish brown. Metasoma black with sternites paler yellowish brown. Anterior two pairs of legs reddish brown with coxae blackish; hind legs black, trochantellus reddish, distal 0.5 of basitarsus and remaining tarsomeres bright yellow. Fore wing blackish with a subapical pale yellowish band; pterostigma black.

*Material Examined* – holotype ♀ *Physotarsus varicornis*, Costa Rica, Guanacaste Prov., Guanacaste National Park, Los Almendros, 100m, viii-ix.1992 (Lopez) (INBio). Syntype ♂, *Scolobates varicornis* Cameron, 1886. Guatemala (BMNH).

*Biological Notes* – *Physotarsus varicornis* has only been collected in Costa Rica. The holotype was collected by net between late August and early September, and the two paratypes were taken in Malaise traps. Although these traps were operated for a total of 36 collecting years only the two specimens of *P. varicornis* were found. Both were taken in the same trap sited in a piece of seven to ten year old regeneration dry forest immediately to the west of the Area Administrativa during June and July, at the beginning of the wet season. *P. varicornis* has a rather striking color pattern, which

suggests it may be a mimic of some common ischnine cryptines such as *Joppidium* species. Its host is unknown.

*Remarks* – Gauld (1997) reported additional specimens: Paratypes: Costa Rica: Guanacaste Prov.: 2 ♀, Santa Rosa National Park, 300 m, vi. 1985, vii.1986 (Gauld & Janzen) (NHM).

Comparisons of the syntype of *varicornis* and the paratype of *davidi* showed that the two species are identical. The syntype of *varicornis* has all the diagnostic features noted by Gauld for *davidi*. Gauld (1997) did not provide comparisons of the newly described Costa Rican species with previously described *Physotarsus* species.

## CHAPTER IV

### GENERIC REVISION OF SCOLOBATINI

#### Overview of Scolobatini

##### Scolobatini Schmiedeknecht, 1911

Scolobatini Schmiedeknecht, 1911: original diagnosis; species descriptions; Townes and Townes (1951): Scolobatini listed as tribe of Scolobatinae. Townes (1970 b): diagnosis, key to genera; generic descriptions; Gauld (1984): diagnosis, key to Australian genera, generic and species descriptions; Graf et al, 1991: discussion of classification, generic and species descriptions.

The tribe Scolobatini, as originally defined by Schmiedeknecht (1911), included only the genus *Scolobates*. This genus was previously placed in the subfamily Banchinae based on the presence in *Scolobates* of strongly pectinate claws. Other genera currently included in the Ctenopelmatinae (Scolobatinae, sensu Townes and Townes, 1951) were then placed in the subfamily Tryphoninae. Definition of the tribe was first modified and expanded by Townes and Townes (1966) and Townes (1970 b), who added two new genera: *Onarion* Townes (1970 b) and *Physotarsus* Townes (1966).

Townes (1970 b) also created a separate tribe, the Westwoodiini, to accommodate a group of four Australian ctenopelmatine genera. Townes (1970 b) did not discuss the relationships among the 8 tribes that he included in the Ctenopelmatinae, and provided no evidence for a close relationship between Westwoodiini and Scolobatini relative to the other tribes. Gauld (1984) treated the Westwoodiini as a synonym of Scolobatini, noting several shared characteristics. The tribe was defined as including the genera *Dictyopheltes*, *Hypopheltes*, *Onarion*, *Pergaphaga*, *Physotarsus*, *Scolobates*, *Tasmabates*, and *Westwoodia*, three of these described as new.

Graf et. al. (1991) described the genus *Catucaba* and discussed its placement in Scolobatini, while Yu and Horstmann (1997), in their catalog of world Ichneumonidae, added the genus *Pionpherta* Aubert, 1993. The inclusion of *Pionpherta* was an error



based on the fact that Aubert (1993) continued to use Scolobatinae as the subfamily name [following Townes (1970 b)], rather than the correct subfamily name Ctenopelmatinae. Yu and Horstmann (1997) mistook Aubert's use of Scolobatinae to mean Scolobatini. It is quite clear from Aubert's (1993) paper that *Pionpherta* is a member of the Pionini and Aubert (1993) characterized his new genus relative to other pionine genera and based the name on the pionine genera *Pion* and *Sympherta*. Gauld (1997) was the last person to treat the Scolobatini when he revised the Ctenopelmatinae of Costa Rica, and described several new species of Scolobatini.

### **Discussion of the revised Scolobatini classification**

#### *Critical assessment of characters previously used to define Scolobatini*

A wide variety of characters have been used in the past to describe the tribe Scolobatini and to delineate it taxonomically. These descriptions varied with the number and the diversity of taxa included within the Scolobatini at the time. The original description of Scolobatini by Schmiedeknecht (1911) included only the genus *Scolobates* Gravenhorst, 1829, so the description of the tribe as a whole corresponded closely to the generic description of *Scolobates*, including characters such as the presence of strongly pectinate claws. Schmiedeknecht (1911) defined the tribe Scolobatini based on the following characters: antennae long with broad flagellomeres, clypeal tooth present medially, and "thick" (broad) hind tarsus.

Tribal description was further modified and expanded by Townes (1970 b), who added two new genera, *Onarion* and *Physotarsus*, to the Scolobatini. Townes (1970 b) characterized the Scolobatini by the lack of the occipital carina on the dorsal 0.35 of head, the occipital and the hypostomal carinae both reaching the base of the mandible, but not joining at or before it; claws pectinate or apparently simple; areolet absent; hind tarsus of male "swollen", whereas that of the female "incrassate", or slightly swollen, more so at the apex; glymma present, but basal and small; epipleurum of tergites 1 and 2 membranous and projecting laterally. Townes (1970 b) noted the significant amount of variation observed in the shape of the clypeal margin among these three genera, as well as the variation in the amount of pectination on claws. Townes' description of the claws

as “apparently simple” is here interpreted as simple apically with some pectination at the very base, a deduction based on the character state observed in *Onarion* and *Physotarsus*.

The epipleurum of tergites 1 and 2 is described by Townes (1970 b) as being membranous and projecting laterally, whereas Gauld (1984, 1997) similarly describes the epipleurum of Scolobatini, but only in reference to tergite 1 of the metasoma. Enlarged and variably membranous epipleurae on the first few metasomal segments are present to various extent in all members of Townes’ Scolobatini, as well as in the genera *Westwoodia*, and, to a lesser extent, *Pergaphaga*. This character was found to be continuous and insufficient for the use in tribal-level taxonomy.

Townes (1970 b) also used two characteristics associated with the occipital and hypostomal carinae in his description of the Scolobatini. One of these, the reduction of the occipital carina at least dorsally, currently remains one of the three diagnostic features of Scolobatini as defined in the present work, with a minor expansion of morphometric measurements of the dorsal reach of the occipital carina from 0.65 to 0.8. Upon close examination, however, the second character, occipital and hypostomal carina both reaching the mandibular base separately, has been transferred from the status of a diagnostic character of Scolobatini, to that of the (*Onarion* + *Physotarsus* + *Catucaba*) clade. The species of *Scolobates* were found to exhibit the condition of joining of the occipital and the hypostomal carinae at the mandibular base, or the hypostomal carina not reaching the mandibular base at all.

In his description of the Scolobatini, Townes (1970 b) indicates that all members of this tribe exhibit sexual dimorphism of the degree of swelling in the hind tibia, males displaying a more pronounced condition. Observations made during the present study suggest that the amount of hind tarsal swelling observed intraspecifically has no indication of sexual dimorphism – both sexes are alike. This character, however, is unique within the Ctenopelmatinae, and although it is not easily delineated morphometrically due to wide variation in ratios of leg components, it is readily obvious when compared to other ichneumonids. The presence of thick and elongate hind tarsi in both sexes is, therefore, a character that is put forth in this study as the second of the three characters that define the Scolobatini. Lastly, the third diagnostic character used here is

also that noted by Townes (1970 b): the absence of 3rs-m vein in the fore wing, thus leaving an open areolet.

Gauld (1984) cleared up a number of nomenclatural problems associated with the Australian genera and provided the first sound delineations of these taxa. Gauld's (1984) character-based assessment was a major step forward in understanding relationships among the scolobatines. Gauld (1984) used the following characters to define the Scolobatini:

1. The possession of a tyloid on the short first flagellar segment
2. The enlarged and invaginated proctodeal membrane of the male
3. The membranous epipleuron of tergite 1
4. The simple convex propodeum.

A detailed review of these characters yielded a reevaluation of the proposed classification.

Antennal tyloids in the Ichneumonidae have been defined as “any type of large raised, flattened or indented sensory area on a flagellar segment” (Gauld 1991). Such structures, located on either male or female flagellomeres, have been reported in 8 subfamilies of Ichneumonidae: Ichneumoninae, Cryptinae, Pimplinae, Tryphoninae, Adelognathinae, Cylloceriinae, Orthocentrinae, and Diplazontinae (Gokman & Krutov 1996). The Scolobatini tyloid referred to in Gauld's (1984) description is located laterally on the 1<sup>st</sup> flagellomere, and is found in both sexes. The tyloid appears to be a variously-arranged patch of multiporous plate sensilla (MPS), sensory structures commonly scattered all along the lateral antennae of ichneumonids (Basibuyuk & Quicke 1998). MPS are thought to have arisen from fusion of two distal setiform sensilla (Basibuyuk & Quicke 1998), although arguments persist as to the exact evolutionary development and function of these structures. A patch-like agglomeration of MPS, however, may also serve a glandular function. A similar “MPS patch tyloid” on the terminal antennal segment of *Trichopria* (Diapriidae) was concluded to be a “spread and release structure” (Isidoro et al 1996). Further cytological and behavioral studies of this particular tyloid are needed for ichneumonids in order to positively resolve the question of function.

Size, shape and number of MPS comprising these tyloids were found to vary among the Scolobatini taxa. The tyloids of *Westwoodia* and *Pergaphaga* (Fig. 84) are

very similar in shape and size, and are comprised of over 50 MPS which appear more rounded in the center, whereas the tyloids of *Physotarsus* (Fig. 85) and *Scolobates* (Fig. 86) appear to consist of 5-10 elongated MPS. Considering the tyloid location on the antennae, as well as the physical size differences among the Australian species (*Westwoodia* and *Pergaphaga*) and the New World species (*Physotarsus* and *Scolobates*), it is concluded here that the microstructure of the tyloid patches is homologous across taxa.

Upon examining other ctenopelmatine taxa, however, tyloid structures nearly identical in location, size, and microstructure have been found in taxa belonging to two other tribes of Ctenopelmatinae: *Perilissus townesi* (Burks, 1952) (Perilissini) (Fig. 87), and *Trematopygodes sp.* (Mesoleiini) (Fig. 88). The tyloids in these other ctenopelmatines are treated here as homologous to those found in the Scolobatini, and thus the utility of the tyloid character to delineate the tribe Scolobatini (sensu Gauld) is problematic.

The second character used by Gauld (1984) to delineate Scolobatini is the presence of an enlarged and invaginated proctodeal membrane in males. Upon specimen examination and personal consultation with Ian Gauld regarding this character, however, it was determined to be of questionable utility. An invaginated, membranous structure is quite difficult to visualize on pinned specimens and special soft tissue preparation is required in order to see the invaginated proctodeal membrane. As such, this character was not found to be useful in scoring the available material, all represented by dry, mounted specimens. A membranous region is clearly visible in most of the large-bodied Australian species but is absent in other large-bodied ctenopelmatines such as members of the genus *Opheltes*. More detailed study of fresh material is needed for adequate delineation of this feature and to ascertain its utility for assessing relationships among the Australian genera. The non-Australian genera differ in appearance, but it is uncertain whether this is due to smaller body size, preparation artifacts, or the absence of a homologous feature.

The presence of a laterally projecting membranous epipleurum is a character used by Townes (1970 b) and Gauld (1984, 1997), and is discussed above. The use of this character in higher-level taxonomy is rejected due to the lack of a clear, unambiguous definition of the character itself, a great difficulty in delineating character states in this

continuous character, and, most importantly, the lack of a membranous and projecting lateral epipleurum in *Dictyopheltes*, *Hypopheltes*, and *Tasmabates*.

Finally, the presence of a simple convex propodeum – the 4<sup>th</sup> character used by Gauld (1984) to define the Scolobatini – is excluded as well due to the lack of an alternate state or discussion in reference to this character in Gauld's work. This character is also excluded in Gauld's subsequent work on Scolobatini (Gauld 1997), leaving the three characters discussed here as the primary delineation of Scolobatini sensu Gauld.

Due to the problematic nature of the characters used by Gauld (1984, 1997) to unite Scolobatini with Westwoodiini, it seems preferable to retain the two as separate tribes following Townes (1970 b). A redefinition for the Scolobatini is therefore proposed.

### **Generic revision of the Scolobatini**

#### *Diagnosis:*

1. Occipital carina incomplete, not reaching 0.8 of head dorsally.
2. Areolet in forewing open, vein 3rs-m absent entirely.
3. Hind tarsus thick, elongate.

*Biology* – parasitoids of various species of Argidae (Gauld, 1997). *Distribution:* New World, Eurasia.

#### *Scolobatini: included genera*

*Catucaba* Graf, Kumagai, Dutra, 1991

*Onarion* Townes, 1970

*Physotarsus* Townes, 1966

*Scolobates* Gravenhorst, 1829

#### *Scolobatini: excluded genera*

*Dictyopheltes* Gauld, 1984

*Hypopheltes* Cushman, 1924

*Pergaphaga* Gauld, 1984

*Tasmabates* Gauld, 1984

*Westwoodia* Brullè, 1846

### **Scolobatini** Schmiedeknecht, 1911

*Description* – gena in lateral view wide, occiput usually strongly declivitous dorsally. Interantennal area smooth, without pronounced ridge. Occipital carina ranges from vestigial to reaching ventral 0.7 of head, never joining hypostomal carina before reaching mandibular base. Antennae with a small oval to amorphous tyloid structure on the lateral outer side of flagellomere 1 (see discussion on tyloids above). Body shiny, with or without punctures. Scutum rounded, sometimes quite convex, notauli absent. Fore wing with Rs+2R originating at mid pterostigma, areolet always open. Abscissa of Cu1 between 1m-cu and Cu1a always shorter than Cu1b. Hind wing with distal abscissa of 1a never reaching the wing margin, sometimes reduced or absent; distal abscissa of cubitella and radiella never complete to wing margin. Transverse carinae of the propodeum always absent, median longitudinal carinae never reaching the anterior margin, pleural carinae variable, propodeum never rugose. Hind tarsi thick, elongate, claws partially to fully pectinate. Gaster with glymma in the form of glymmal group 1 (Fig. 89), dorso-median tendonal juncture is slightly to quite distinctly sloped. Tergite 1 rectangular to sub-trapezoidal, 1.5-3.0 times as long as posteriorly broad, without median longitudinal carinae, lateral longitudinal carinae never extending beyond spiracle. Abdominal segments with no heavy sclerotization, membranous at parts. Cerci sessile to quite prominent, attached dorsally to the middle of posterior aspect of gaster.

### **Scolobatini taxa**

#### ***Catucaba* Graf, Kumagai, Dutra, 1991**

*Type species:* *Catucaba anatterae* Graf, Kumagai, Dutra, 1991.

*Description* – length: body 2.5-4.1 mm, fore wing 2.9-4.2 mm. Head: Clypeal margin thin, sharp, somewhat to distinctly trapezoid, medially without a thick central lobe or a median tooth. Clypeus 2.0-2.5 times as long as wide, apically flat to slightly impressed, with two small basolateral lobes weakly protruding in profile, not separated

from face. Anterior tentorial pits elongated and turned ventrad. Malar space 0.5-0.6 times basal width of mandible, mandible with lower tooth slightly longer than the upper, mandible tapering over basal 1/3 to 1/2, sides almost parallel apically. Face punctures quite deep, denser anteromedially, 1.1-1.4 as broad as long, not terminating dorsally with a median tooth. Interantennal area slightly concave, anterior margin of torulus situated at about 0.75 of eye height. Widest diameter of torulus about equal widest diameter of median ocellus. Area between lateral ocelli strongly depressed, distance between lateral ocelli 1.1-1.5 times their widest diameter, distance from lateral ocellus to eye margin 1.8-2.2 times its widest diameter. Area behind ocelli regularly rounded, not sharply declivitous. Antennae quite long, number of flagellomeres varies from 30 to 35. First flagellomere with a small tyloid laterally, length of tyloid 1.0-1.3 times widest transverse diameter of eye, second flagellomere is 0.6 times length of first. Occipital carina incomplete, present on the ventral 0.5 of head, never joining hypostomal carina at or before mandibular base. Pronotum somewhat depressed dorsally, strongly downturned laterally, anterior margin of the pronotum strongly emarginate medially, rounded and upcurved laterally. Lateral groove of the pronotum narrow, vestigial to quite prominent, never complete. Pronotum smooth, shiny. Scutum glabrous, strongly convex, very light punctures present on the anterolateral 0.4, notauli absent. Epicnemial carina extends along ventral 0.3 of pronotum, reaching anterior margin of mesopleuron. Mesopleuron always lightly pubescent ventrally, punctures absent on dorsal 0.3. Propodeum with pleural carinae absent, lateral longitudinal carinae vestigial at base, median longitudinal carina absent, lightly pubescent laterally, smooth and impunctate medially. Trochanter 4.2-4.4 times as long as basally wide, apical margin of trochanter not reaching the apical margin of trochantellus. Pretarsus equal in length to tarsomere 4. Claws lightly pectinate at the very base. Forewing with abscissa of Cu1 between 1m-cu and Cu1a about 0.25-0.35 times the length of Cu1b. Marginal cell about 3.1-3.9 times as long as wide. Hind wing with distal abscissa of 1a entirely absent. Tergite 1 about 1.7 times as long as broad, spiracles flat. Cerci quite prominent.

*Color* – patterned in shades of dark-brown to black and light-yellowish to white.

*Distribution* – restricted to the Neotropics, known from Brazil and Argentina.

*Biology* – unknown.

*Variation* – all specimens of both species of *Catucaba* examined by the author are quite uniform in coloration and morphology. Specimens not included in the description of *Catucaba montanica* exhibit very similar morphological features, but are 2/3 the size of the smallest described *Catucaba*. No male specimens were examined. Female specimens exhibited prominent size dimorphism, it is possible that smaller and otherwise morphologically identical specimens are a different species. More material is needed in order to make that determination.

*Diversity* – this genus is small, containing 2 species.

***Catucaba anatterae* Graf, Kumagai, and Dutra, 1991**

(Figs 64, 65)

*Catucaba anatterae*, Graf, Kumagai, and Dutra, 1991. Yu and Horstmann (1997): catalog, p. 455.

*Diagnosis* – lateral ocelli separated by 1.5 times their widest diameter from each other, and by about 2.2 times their widest diameter from the eye margin. Antenna with 35 flagellomeres. Lateral groove of the pronotum present on the dorsal 0.5-0.6. Mesopleuron punctation moderate, present on the ventral 0.7. Forewing with marginal cell about 3.9 times as long as wide. Antennae uniformly brownish, hind tarsi black.

*Description: Female* – body (Fig. 64) 4.1 mm, fore wing 4.2 mm Head (Fig. 65): Clypeal margin thin, sharp, somewhat trapezoid, medially without a thick central lobe. Clypeus 2.0 times as long as wide, apically flat to slightly impressed, with two small basolateral lobes weakly protruding in profile. Clypeus, mandibles and face quite densely covered by long setae. Anterior tentorial pits exceptionally elongate, very narrow, downturned. Malar space 0.6 times width of mandibular base. Face about 1.4 times as broad as long, not terminating dorsally with a median tooth; punctures deep and dense, more so anteromedially, face pubescent. Interantennal area somewhat concave laterally, area immediately behind antenna uniformly concave, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.75 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus about



equal widest diameter of median ocellus. Lateral ocelli separated by 1.5 times their widest diameter from each other, and by about 2.2 times their widest diameter from the eye margin. Area between lateral ocelli slightly depressed. Area behind ocelli not sharply declivitous. Antenna with 35 flagellomeres, length of first flagellomere about 1.3 times widest transverse diameter of eye; second flagellomere about 0.6 times the length of first. Occipital carina present on the ventral 0.5 of head, not joining hypostomal carina at mandibular base. Mesosoma: Anterior margin of the pronotum medially moderately bifurcate, laterally rounded and slightly upcurved. Pronotum depressed dorsally, strongly downturned laterally; impunctate. Lateral longitudinal groove of the pronotum present on the dorsal 0.5-0.6. Scutum shiny, strongly convex, very sparsely punctured on the anterolateral 0.4. Epicnemial carina strong, extends along ventral 0.3 of pronotum, reaching the anterior margin of mesopleuron. Mesopleuron punctation moderate, present on ventral 0.7. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.25 times length of Cu1b. Marginal cell about 3.9 times as long as wide. Propodeum with posterior vestige of lateral longitudinal carinae, impunctate medially, sparsely pubescent laterally. Claws simple. Metasoma: T1 about 1.7 times as long as broad. Cerci protruding.

*Male* – none.

*Color* – white and light to dark-brown. Antennae uniformly brownish, hind tarsi black. Wings hyaline.

*Material Examined* – 1 female (paratype).

*Biological Notes* – host unknown, species from Brazil.

***Catucaba montanica* Zhaurova, spec. nov.**

(Figs. 66, 67)

*Diagnosis* – lateral ocelli separated by about 1.1 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Antenna with 30-31 flagellomeres. Epomia present on the dorsal 0.4 of the pronotum. Mesopleuron very lightly punctate ventrally. Forewing with marginal cell about 3.1-3.2 times as long as wide. Flagellomeres 13-15 white, rest of flagellum brownish. Hind tarsus black basally, apical 3 tarsomeres white.

*Description: Female* – body (Fig. 66) 2.5-4.1 mm, fore wing 2.9-4.0 mm. Head (Fig. 67): clypeal margin thin, sharp, distinctly trapezoid, medially without a thick central lobe. Clypeus 2.5 times as long as wide, apically flat to slightly impressed, with two small basolateral lobes weakly protruding in profile. Clypeus, mandibles and face quite densely covered by long setae. Anterior tentorial pits exceptionally elongate, very narrow, downturned. Malar space 0.5-0.6 times width of mandibular base. Face about 1.1 times as broad as long, not terminating dorsally with a median tooth; punctures dense, more so anteromedially. Interantennal area somewhat concave, area immediately behind antenna uniformly concave, turning convex before reaching ocelli. Anterior margin of torulus situated at about 0.75 of eye height. Interantennal distance greater than the distance between lateral ocelli. Widest diameter of torulus about equal widest diameter of median ocellus. Lateral ocelli separated by about 1.1 times their widest diameter from each other, and by about 1.8 times their widest diameter from the eye margin. Area between lateral ocelli strongly depressed. Area behind ocelli not sharply declivitous. Antenna with 30-31 flagellomeres, length of first flagellomere about equal widest transverse diameter of eye; second flagellomere about 0.6 times length of first. Occipital carina present on the ventral 0.5 of head, not joining hypostomal carina at mandibular base. Mesosoma: Anterior margin of the pronotum medially strongly emarginate, laterally rounded and slightly upcurved; pronotum depressed dorsally and strongly downturned laterally; pronotum impunctate. Lateral longitudinal groove of the pronotum present on dorsal 0.4. Scutum shiny, strongly convex, very sparsely pubescent on anterolateral 0.4. Epicnemial carina strong, extends along ventral 0.3 of pronotum, reaching anterior margin of mesopleuron. Mesopleuron very lightly punctate ventrally. Fore wing with abscissa of Cu1 between 1m-cu and Cu1a about 0.3 times length of Cu1b. Marginal cell about 3.1-3.2 times as long as wide. Propodeum with posterior vestige of lateral longitudinal carinae, impunctate medially, lightly punctured laterally. Claws simple. Metasoma: T1 about 1.7 times as long as broad. Cerci protruding.

*Male* – none.

*Color* – light-yellowish and white with brown to black markings. Wings hyaline. Flagellomeres 13-15 white, rest of flagellum brownish. Hind tarsus black basally, apical 3 tarsomeres white.

*Material examined* –5 females. Holotype: ♀, M. Gerals, Varginha, Brazil, II-1972, (M. Alvarenga); Paratypes: 3 ♀, Represa Rio Grande, Guanabara, Brazil, X-1969, (M. Alvarenga); 1 ♀, Represa Rio Grande, Guanabara, Brazil, XII-1967, (M. Alvarenga).

*Biological notes* – host unknown, species probably inhabits high elevation habitat.

### ***Onarion* Gauld 1993**

(Figs. 68-70)

*Type species: Onarion plaumanni* Townes, 1970.

*Description* – length: body: 4.9-9.3 mm (Fig. 68), fore wing 5.0-9.5 mm. Clypeal margin blunt laterally, with a slightly protruding median tooth (Fig. 69). Clypeus about 2.1-2.3 times as wide as long, flat in profile, not distinctly separated from face. Anterior tentorial pits oval, with lateromost corners downturned. Malar space about equal in length to basal width of mandible. Mandible with lower tooth slightly longer than the upper, lower tooth distinctly separated into an upper blunt area and a lower extended apex, sides almost parallel. Dorsal margin of mandible with a distinct median convexity. Mouthparts haustellate (Fig. 70). Face smooth, lightly to quite strongly pubescent, 0.9 to 1.1 times as wide as long, with a median tooth dorsally. Interantennal area flat to narrowly raised medially, anterior margin of torulus situated at about 0.6-0.7 of eye height. Widest diameter of torulus slightly wider than widest diameter of median ocellus. Area between lateral ocelli flat to slightly depressed, distance between lateral ocelli 0.7-1.1 times their widest diameter, distance from lateral ocellus to eye margin 1.2-1.5 times its widest diameter. Area behind ocelli sharply declivitous. Antennae quite long, number of flagellomeres variable. First flagellomere with a small tyloid laterally, length of second flagellomere 0.6-0.8 times length of first. Occipital carina present, extremely vestigial at mandibular base, never joining hypostomal carina at or before mandibular base. Pronotum broadly rounded to truncate anteriorly, flat to slightly emarginate medially, lateral margin of the pronotum sharp, epomia usually vestigial dorsally. Pronotum usually impunctate. Scutum glabrous, pubescence extremely sparse or absent, notauli absent. Epicnemial carina extends along ventral 0.3 of pronotum, inclined to, but never reaching

anterior margin of mesopleuron. Mesopleuron lightly pubescent, smooth to very lightly punctured. Propodeum with pleural carinae posteriorly vestigial, lateral longitudinal carinae sometimes present as posterior vestiges; impunctate, laterally pubescent. Posterolateral edge of propodeum somewhat upcurved. Apical margin of trochanter reaching the apical margin of trochantellus. Pretarsus longer than tarsomere 4. Claws fully pectinate. Forewing with abscissa of Cu1 between 1m-cu and Cu1a about 0.7-0.8 times length of Cu1b. Marginal cell about 3.1 times as long as wide. Hind wing with distal abscissa of 1a extremely vestigial, not reaching beyond 0.3 ways to the wing margin. Tergite 1 about 2.2-2.3 as long as posteriorly broad, spiracles slightly protruding in profile. Cerci quite prominent. Genital plate in female broader than in male.

*Color* – shades of yellow and brown, wings hyaline to yellowish, distal part sometimes brownish-infumate

*Distribution* – restricted to the New World, occur between Panama and Southern Brazil.

*Biology* – host unknown.

*Variation* – all species examined are extremely similar in color and morphology, main species characters are largely morphometric.

*Diversity* – this genus contains 2 described species: *O. plaumanni* and *O. masneri*, as well as 3 undescribed species (Gauld 1997, personal observations).

### ***Physotarsus* Townes, 1966**

See Chapter III

### ***Scolobates* Gravenhorst, 1829**

(Figs. 71, 72)

*Type species: Scolobates auriculatus* Fabricius, 1804.

*Description* – length: body: 5.3-10.4 mm (Fig. 71), fore wing: 4.6-9.8 mm. Clypeal margin blunt laterally, with a slightly protruding median tooth (Fig. 72). Clypeus about 2.3-3.2 times as wide as long, apically protruding and basally slightly concave in

profile, not distinctly separated from face. Anterior tentorial pits oval, with lateromost corners downturned. Malar space about 1.2-1.4 times longer than basal width of mandible. Mandible with the lower tooth slightly longer than the upper, lower tooth distinctly separated into an upper blunt area and a lower extended apex. Mandible triangular, wide at base and narrowing at apex. Dorsal margin of mandible without a distinct median convexity. Face smooth or lightly punctured, lightly to quite strongly pubescent, 1.3-1.4 times as wide as long, with a median tooth dorsally. Interantennal area flat to slightly raised medially, anterior margin of torulus situated at about 0.6-0.7 of eye height. Widest diameter of torulus slightly wider than widest diameter of median ocellus. Area between lateral ocelli flat to slightly depressed, distance between lateral ocelli 0.7-1.2 times their widest diameter, distance from lateral ocellus to eye margin 1.3-2.1 times its widest diameter. Area behind ocelli sharply declivitous. Antennae quite long, number of flagellomeres variable. First flagellomere with a small tyloid laterally, length of second flagellomere 0.6-0.7 times length of first. Occipital carina present on the ventral 0.4 of head, occipital and hypostomal carina join at mandibular base, or hypostomal carina terminates just before mandibular base. Pronotum broadly rounded to truncate anteriorly, flat to strongly emarginate medially, lateral margin of the pronotum sharp, lateral longitudinal groove of the pronotum absent entirely to complete. Pronotum impunctate. Scutum glabrous, pubescence sparse or absent, notauli absent. Epicnemial carina extends along ventral 0.3 of pronotum, never reaching anterior margin of mesopleuron. Mesopleuron pubescent, smooth to lightly punctured. Propodeum with pleural carinae complete, lateral and median longitudinal carinae present in some species, alone or in combination, entirely absent in others; propodeum largely impunctate, quite strongly pubescent laterally, lightly pubescent or smooth medially. Posterolateral edge of propodeum upcurved. Apical margin of trochanter reaching the apical margin of trochantellus. Pretarsus longer than tarsomere 4. Claws fully pectinate. Forewing with abscissa of Cu1 between 1m-cu and Cu1a about 0.6-0.8 times length of Cu1b. Marginal cell about 3.0-3.2 times as long as wide. Hind wing with distal abscissa of 1a reaching at least half way to wing margin, but never reaching the margin in the form of a tubular vein. Tergite 1 about 2.0-2.7 as long as posteriorly broad, spiracles flat. Cerci variable, usually quite prominent.

*Color* – variable.

*Distribution* – recorded in Canada and US, as far south as TX. Old World: Europe through Japan, and from Turkey in the Middle East.

*Biology* – some species recorded to attack sawflies of genus *Arge* (Argidae).

*Variation* – all species examined are extremely similar in color and morphology, main species characters are largely morphometric.

*Diversity* – this genus contains 11 described species, and at least as many undescribed. Due to its wide Palearctic, Oriental, and Nearctic distribution, the actual number of species has a potential to be quite high.

### **Generic revision of the Westwoodiini**

#### **Westwoodiini Townes, 1969, new status**

Westwoodiini Townes, 1969. Original diagnosis, redescription of the genera. Gauld (1984): tribe synonymized with the Scolobatini.

*Remarks* – Fitton and Gauld (1976) changed Westwoodiini Townes, 1970 b to Megaceriini Szepligeti, 1908, based on nomenclatural priority. Townes (1970 b) previously mistakenly included the genus *Megaceria* Szepligeti, 1908 in this tribe due to a misidentified specimen. The drawings accompanying the redescription of this genus indicate that Townes' (1970 b) redescription of *Megaceria* pertains to a genus later described by Gauld (1984) as *Pergaphaga*. The genus *Megaceria* was subsequently transferred to the Euryproctini (Gauld 1984).

#### *Diagnosis:*

1. Area between antennae with a prominent ridge.
2. Forewing vein Rs+2r originates at proximal end of pterostigma.
3. Cerci attached ventrad to the middle of posterior aspect of gaster.

*Biology* – parasitoids of various species of sawflies Pergidae (Gauld 1984).  
Limited to Australia in distribution.

*Westwoodiini: included genera:**Dictyopheltes* Gauld, 1984*Hypopheltes* Cushman, 1924*Pergaphaga* Gauld, 1984*Westwoodia* Brullè, 1846*Westwoodiini: excluded genera:**Megaceria* Szepligeti, 1908*Tasmabates* Gauld, 1984**Westwoodiini** Townes, 1969

*Description* – gena in lateral view wide, strongly declivitous. Interantennal area bears a prominent ridge. Occipital carina always complete, always joining hypostomal carina before reaching mandibular base. Antennae with a large round or oval tyloid structure on the lateral outer side of flagellomere 1. Body shiny or matte and coarse, with or without punctures. Scutum rounded, never strongly convex, notauli present, strong, sometimes reaching the anterior margin of mesoscutum. Fore wing with Rs+2R originating at near proximal end of pterostigma, areolet usually closed, petiolate. Hind wing with distal abscissae of 1a, radiella and cubitella all reaching the wing margin. Transverse carinae of the propodeum sometimes present, pleural carina always complete, median and lateral longitudinal carinae usually present, though vestigial; propodeum varying from completely smooth and impunctate, to rugose. Apical margin of trochanter reaching the apical margin of trochantellus. Hind tarsi not significantly thickened or elongate, claws simple. Gaster with glymma in the form of glymmal group 1 and 2 (Figs. 89, 90), dorso-median tendonal juncture of variable shape. Tergite 1 quite variable in shape, usually impunctate. Abdominal segments membranous to quite heavily sclerotized. Cerci sessile to quite prominent, attached ventrally to the middle of posterior aspect of gaster. Species large, slender, coloration orange, black or brownish.

## Westwoodiini Taxa

### ***Dictyopheltes* Gauld, 1984**

(Figs. 73, 74)

*Type species: Dictyopheltes robustus* Gauld, 1984.

*Description* –length: body 12-13.5 mm (Fig. 73), fore wing 10-13 mm. *Head* (Fig. 74): clypeal margin thin, slightly protruding, truncate. Clypeus 2.2-2.4 times as broad as long, convex in profile, punctate to slightly rugose, with a prominent median transverse sulcus. Anterior tentorial pits fairly small, prominent. Malar space 0.6-1.1 times basal width of mandible, mandible with lower tooth slightly longer than upper, sides parallel at the apical 2/3. Face 2.2-2.9 times as broad as long, terminating dorsally with a median tooth; face evenly punctured, punctures deep and dense. Interantennal area with a prominent ridge that extends beyond the posterior margin of toruli, splitting into 3 forked processes. Post-antennal area concave laterally, turning convex before reaching ocelli. Widest diameter of torulus about 1.3-1.4 times widest diameter of median ocellus. Area between lateral ocelli depressed and then slightly raised laterally, distance between lateral ocelli 1.6-1.8 times their widest diameter, distance from lateral ocellus to eye margin 1.8-2.0 times its widest diameter. Area behind ocelli regularly rounded, slightly raised medially. Antennae with 32 flagellomeres, length of first flagellomere 1.6 times widest transverse diameter of eye, second flagellomere about equal length of first. Occipital carina complete, joining the hypostomal carina above base of mandible. Pronotum strongly depressed dorsally, epomia present, not very distinct due to the overall strongly punctured to rugose texture of the pronotum. Scutum quite strongly raised, densely punctured anteriorly, punctures not as dense posteriorly; notauli quite prominent, arising just past the anterior margin of scutum, not reaching its posterior margin. Epicnemial carina extends along ventral 0.2 of pronotum, not reaching anterior margin of mesopleuron. Propodeum rugose, strongly convex and quite narrow longitudinally, with pleural carinae complete, median and lateral longitudinal carinae vestigial posteriorly, transverse carinae absent, tibia and tarsus slender, claws simple. Forewing with areolet



closed, petiolate, or with 3 r-m absent; cu-a almost opposite base of Rs&M, vertical; marginal cell slender; first sub-discal cell not explanate distally. Hind wing with first abscissa of Cu1 slightly shorter than cu-a. Tergite 1 less than 2.0 times as long as posteriorly broad, sternite 1 reaching at most 0.5 of distance to spiracle. Glymma present, group 2 (Fig. 90)

*Color* – mostly black with some orange-brown.

*Distribution* – restricted to Australia.

*Biology* – unknown.

*Etymology* – *Dictyos* = a net, referring to the propodeal sculpture; *Opheltes* = a related genus. Masculine. (Gauld 1984).

*Remarks* – a distinct genus on account of the presence of a median transverse sulcus on the clypeus, as well as anteriorly incomplete notauli.

### ***Hypopheltes* Cushman, 1924**

(Figs. 75, 76)

*Type species: Hypopheltes pergae* Cushman, 1924.

*Description* – length: body 15-19 mm (Fig. 75), fore wing 14-21 mm. Clypeal margin thin, widely truncate (Fig. 76). Clypeus 2.0-2.2 times as broad as long, convex in profile, lightly to moderately punctured, without a median transverse sulcus. Anterior tentorial pits elongate and prominent, such that the clypeus is raised medially and concave laterally. Malar space 0.2-0.6 times basal width of mandible base, mandible with lower tooth slightly longer than upper, sides parallel over apical 2/3. Face 1.9-2.1 as broad as long, terminating dorsally with a small median tooth; face deeply densely punctured, slightly rugose medially. Interantennal area with a prominent ridge that extends posteriorly, splitting into 2 processes beyond the posterior margin of torulus. Post-antennal area concave laterally. Widest diameter of torulus about equal widest diameter of median ocellus, ocelli large and raised. Area between lateral ocelli slightly to moderately depressed medially, ocelli large and very close to one another, distance between the eye margin and lateral ocellus 0.6 times its widest diameter. Area behind

ocelli regularly rounded. Antennae with 39-45 flagellomeres, length of first flagellomere about 0.8 times widest transverse diameter of eye, second flagellomere about as long as first. Occipital carina complete, joining the hypostomal carina above base of mandible.

Pronotum quite strongly depressed dorsally, epomia present, indistinct. Scutum quite strongly raised, sometimes lightly punctured, notauli deep, almost reaching posterior margin of mesoscutum. Epicnemial carina extends along ventral 0.3 of pronotum, not reaching the anterior margin of mesopleuron. Propodeum quite strongly convex, carinae variable, transverse carination present in some species; propodeum never rugose. Tibia and tarsus slender, claws simple. Fore wing with areolet closed, sessile or petiolate; 3r-m always slightly longer than 2r-m; cu-a opposite or distal to base of Rs&M, almost vertical; marginal cell relatively slender; first subdiscal cell not explanate distally. Hind wing with first abscissa of Cu1 slightly shorter than cu-a. Glymma present, group 2 (Fig. 90) tergite 1 with spiracles protruding.

*Color* – black and white, orange.

*Distribution* – restricted to Australia and South-Western New Guinea.

*Biology* – host records: *H. pergae* – Pergidae: *Perga* sp. (Cushman 1924); *H. sp.* – Pergidae: *Pseudoperga belinda* Kirby (Gauld 1984).

*Remarks* – this genus currently contains one described and one undescribed species. Males are noticeably smaller than females.

### ***Pergaphaga* Gauld, 1984**

(Figs. 77, 78, 84)

*Type species: Pergaphaga nigra* Gauld, 1984.

*Description* –length: body 10.5-18.7 mm (Fig. 77), fore wing 10-17 mm. *Head* (Fig. 78): clypeal margin thin, flat, widely truncate. Clypeus 2.5-2.7 times as broad as long, slightly convex in profile, punctate to transversely rugose, without a median transverse sulcus. Anterior tentorial pits fairly small, elongate. Malar space 0.4-0.6 times basal width of mandible, mandible with lower tooth slightly longer than the upper, or mandibular teeth equal in length, sides parallel over apical 2/3. Face 1.5-1.6 times as broad as long, terminating dorsally with a median tooth; face strongly punctured,

sometimes covered by dense white setae. Interantennal area with a prominent raised ridge that extends beyond posterior margin of toruli, splitting in to 3 forked processes, middle process sometimes not as distinct. Post-antennal area quite deeply concave laterally, turning convex before reaching ocelli. Widest diameter of torulus about 1.3-1.5 times widest diameter of median ocellus, ocelli fairly small, not distinctly raised. Area between lateral ocelli quite strongly depressed medially, distance between lateral ocelli 1.6-2.0 times their widest diameter, distance from lateral ocellus to eye margin 1.6-2.1 times its widest diameter. Area behind ocelli regularly rounded, slightly raised medially. Antennae with flagellum quite long, slender, length of first flagellomere 1.3 times widest transverse diameter of eye, second flagellomere about equal length of first. Occipital carina complete, joining the hypostomal carina above base of mandible. Pronotum strongly depressed dorsally, epomia present, indistinct. Scutum quite strongly raised, densely punctured, notauli quite prominent, arising at anterior margin of scutum, almost reaching its posterior margin. Epicnemial carina extends along ventral 0.2 of pronotum, not reaching anterior margin of mesopleuron. Mesopleuron densely punctured ventrally and dorsally, punctures not as dense posteromedially. Propodeum rugose, strongly convex and quite narrow longitudinally, pleural carinae complete, median and lateral longitudinal carinae vestigial posteriorly, anterior transverse carina quite distinct, sometimes raised, posterior transverse carina sometimes present medially. Tibia and tarsus slender, claws simple. Fore wing with areolet closed, petiolate, or absent entirely, cu-a opposite or distal to Rs&M, almost vertical so that upper inner corner of first subdiscal cell is about 75°; marginal cell narrow; first sub-discal cell not or only slightly explanate distally. Hind wing with first abscissa of Cu1 shorter than cu-a. Tergite 1 long and slender anteriorly, widening distally beyond spiracles, 2.2 or more times as long as posteriorly broad, sternite 1 reaching 0.6 of distance to spiracle. Glymma present, group 2 (Fig. 90)

*Color* – mostly black with some orange-brown.

*Distribution* – restricted to Australia.

*Biology* – host records: *P. nigra* – Pergidae: *Perga* sp.; *Perga affinis* Kirby.

*Pergaphaga* sp. 1 – Pergidae: *Pergagraptia gravenhorstii* (Westwood); *P. bella* Newman. (Gauld 1984).

*Etymology* – Perga (from the host genus of sawfly) and “phaga” (to eat). (Gauld 1984).

*Remarks* – this genus is fairly small. One species is described, but according to Gauld (1984), there are three more undescribed species.

***Westwoodia* Brullè, 1846**

(Figs. 79-83)

*Type species: Westwoodia ruficeps* Brullè, 1846.

*Description* –length: body 8.3-16.4 mm (Fig. 79), fore wing 8.5-15.3 mm. *Head* (Fig. 80): clypeal margin slightly thickened, flat, widely truncate. Clypeus 2.7-2.9 times as broad as long, convex in profile, without a median transverse sulcus (Fig. 80). Anterior tentorial pits oval. Malar space 1.2-1.3 times basal width of mandible, mandible with lower tooth slightly longer than the upper, sides parallel over apical 2/3. Face 1.8-2.0 times as broad as long, terminating dorsally with a median tooth; surface lightly to moderately punctate, setose. Interantennal area with a prominent raised ridge that extends beyond posterior margin of toruli, terminating at median ocellus, two additional lateral ridges present in some species. Post-antennal area deeply excavated. Widest diameter of torulus about 1.3-1.4 times widest diameter of median ocellus, ocelli fairly small, not distinctly raised. Area between lateral ocelli depressed medially, distance between lateral ocelli 0.9-1.3 times their widest diameter, distance from lateral ocellus to the eye margin is 1.4-2.3 times its widest diameter. Area behind ocelli rounded to quite sharply declivitous. Antennae with flagellum quite long, slender, length of first flagellomere 0.8 times widest transverse diameter of eye, second flagellomere about 0.7-0.8 times length of first. Occipital carina complete, joining the hypostomal carina above base of mandible (Fig. 83). Pronotum quite strongly depressed dorsally, epomia usually absent. Scutum quite strongly raised, impunctate, notauli quite prominent, arising at anterior margin of scutum, reaching to posterior 0.6-0.7 of scutum. Epicnemial carina extends along ventral 0.2 of pronotum, not reaching anterior margin of mesopleuron. Mesopleuron largely impunctate. Propodeum smooth, lightly setose laterally, quite strongly convex, pleural

carinae complete, median and lateral longitudinal carinae vestigial posteriorly, transverse carinae absent. Tibia and tarsi flattened laterally, posteroventral-most corners of tarsomeres 1-4 extended; tarsomeres fairly short, wide, claws simple. Fore wing with areolet closed, petiolate, with 3r-m only slightly shorter than 2r-m, or with 2r-m absent; marginal cell slender; first subdiscal cell not explanate distally. Hind wing with first abscissa of Cu1 slightly shorter than cu-a; distal abscissa of Cu1 strong. Tergite 1 with sides parallel to trapezoid, 1.7-2.1 times as long as posteriorly broad, sternite 1 reaching 0.3-0.4 of distance to spiracle. Glymma present, group 1 (Fig. 89)

*Color:* Mostly black and orange-brown. Abdominal segments sometimes white posteriorly.

*Distribution* – restricted to Australia.

*Biology* – *W. ruficeps* – Pergidae: *Pseudoperga* sp. (Gauld 1984).

*Etymology* – after Westwood.

*Remarks* – this genus is fairly small, containing two described species. Gauld (1984) suggested that eggs of *Westwoodia* are exceptionally large. Dissection of the female abdomen of a specimen of *W. ruficeps* revealed numerous small, weakly-sclerotized eggs, similar to those of other ctenopelmatines (Fig. 81), and much smaller than those of *Netelia* spp.

## CHAPTER V

### PHYLOGENETIC ANALYSES OF *PHYSOTARSUS* TOWNES, 1966

Two separate phylogenetic analyses are presented in this study: a species-level analysis of *Physotarsus* and associated Neotropical genera (topologies: Table 3-5), and a generic analysis of all taxa previously included in Scolobatini (topology: Table 7). Only a few selected taxa from the *Physotarsus* analysis were included in the analysis of scolobatine genera.

#### Included taxa

Where available, several specimens were used of each species to insure adequate assessment of intraspecific variation. However, because many species are poorly represented in collections, almost 1/3 of all codings were made using no more than 1-3 specimens. The use of fewer specimens in coding may inadequately represent the full extent of diversity within a taxon, however, character definitions presented here partially account for this. All terminal taxa represent distinct species.

#### List of taxa included in the phylogenetic analysis of *Physotarsus*: Part 1

1. *Catucaba anatterae* Graf, Kumagai & Dutra, 1991
2. *Catucaba montanica* Zhaurova, 2006
3. *Hypopheltes pergae* Cushman, 1924
4. *Onarion masneri* Gauld, 1997
5. *Onarion plaumanni* Townes, 1970
6. *Physotarsus adrianni* Gauld, 1997
7. *Physotarsus albus* Zhaurova, 2006
8. *Physotarsus castilloi* Gauld, 1997
9. *Physotarsus claviger* Zhaurova, 2006
10. *Physotarsus concavus* Zhaurova, 2006
11. *Physotarsus cordatus* Zhaurova, 2006
12. *Physotarsus eliethi* Gauld, 1997
13. *Physotarsus emarginatus* Zhaurova, 2006

14. *Physotarsus flavipennis* Zhaurova, 2006
15. *Physotarsus foveatus* Zhaurova, 2006
16. *Physotarsus gineus* Zhaurova, 2006
17. *Physotarsus glabellus* Zhaurova, 2006
18. *Physotarsus laucos* Zhaurova, 2006
19. *Physotarsus luteus* Zhaurova, 2006
20. *Physotarsus maculipennis* (Cresson, 1874)
21. *Physotarsus melipennis* Zhaurova, 2006
22. *Physotarsus melotarsus* Zhaurova, 2006
23. *Physotarsus niveus* Zhaurova, 2006
24. *Physotarsus oculatus* Zhaurova, 2006
25. *Physotarsus tonicus* Zhaurova, 2006
26. *Physotarsus truncatus* Zhaurova, 2006
27. *Physotarsus varicornis* Cameron, 1886
28. *Scolobates auriculatus* Fabricius, 1804
29. *Scolobates testaceus* Morley, 1913
30. *Scolobates longicornis* Gravenhorst, 1829
31. *Scolobates species 1* (Japan)
32. *Scolobates species 2* (Taiwan)
33. *Scolobates species 3* (Turkey)
34. *Westwoodia ruficeps* Brullè, 1846.

## Characters

### *Character treatment and character state coding*

Characters and matrices were compiled using the database system created and maintained by Matt Yoder and Krishna Dole (<http://peet.tamu.edu>). A total of 30 characters and 34 OTUs were used in the generic analyses, which were conducted using “WinClada” software (WinClada 2002). All but 1 characters were treated as unordered, and no character weighting was employed. No ambiguities were encountered, thus only one character state was scored per matrix cell.

Characters were mapped on the resulting phylogenies using solid black circles to represent the diagnostic character states, and white circles to represent non-diagnostic character states. All characters mapped on to the phylogeny are unambiguous. Character number is indicated above the branch, whereas the corresponding character state is indicated below it. The transition rate of character states was set as an “unspecified” for all characters. Character number 1, which pertains to the length of the distal abscissa of hind wing vein 1A, is very important in current taxonomy of this group. This character, therefore, was the only one treated as “ordered”, due to its continuous nature.

Slow vs. fast transition rates refer to two alternative hypotheses demonstrating the character state transition in relation to the overall speciation events. When such ambiguity arises, the character is not mapped on the resulting phylogeny. In this case the transition from character state 0 to 1 was placed at the last possible branch node, or at the base of the *Onarion* – *Scolobates* clade.

Wide variation is observed among various species of *Physotarsus*, making species-level phylogenetic analyses quite complex. As compared to the character set included in the generic analyses, states coded for characters employed in the analyses of relationships within *Physotarsus* encompass distinctly less morphological variation. Some characters are used unchanged in both sets of analyses, however, most characters exhibit wide variation in character states.

#### *Presentation format*

Characters are organized in morphological categories: Head, prothorax, mesothorax, legs, wings, and metathorax. In front of each character, in bold font, is the character number referenced to the corresponding character number in the matrix. The Consistency index (CI) and the Retention index (RI) scores follow the character number and are presented as such: 50/75, where 50 is the CI, and 75 is the RI. Following the character states are some remarks regarding the character/character state definition, overall character utility, as well as the variation among and within character states in taxa used in these analyses.



*Head***13** Median region of clypeal margin 50/76

- (0) thick, not, or barely protruding ventrally beyond the apical margin (Fig. 5)
- (1) thick, conspicuously protruding ventrally beyond the apical margin (Fig. 6)
- (2) thick, significantly protruding outwards beyond apical margin (Fig. 7)
- (3) thin, even, not protruding beyond apical margin (Fig. 88)
- (4) ventrally elongate, tooth-shaped (Fig. 8)

The morphology of the clypeal margin is a very important character for delineating and understanding the relationships of both species and genera. Although quite complex, this character accurately encompasses the diversity among species and closely-related genera of Scolobatini (*sensu novo*).

**11** Mouthparts 100/100

- (0) not haustellate (Fig. 82)
- (1) haustellate (Fig. 70)

The term “haustellate” is used here to indicate the extensive mouthpart modifications observed in some taxa that are suspected to be flower-feeding as adults. These modifications include an elongation of labium and maxillae (Fig. 70).

**21** Mandible: shape 100/100

- (0) triangular, gradually narrowing from base to apex
- (1) tapering 1/3 to 1/2 ways basally, sides almost parallel at apex

(2) sides parallel at apical 2/3, basal 1/3 quite strongly tapered

Another apparently important aspect of mandibular shape is the ratio of its base to length (at its longest point). Surprisingly, however, little phylogenetic information was found to be contained in such a character, due to wide interspecific and intraspecific variation in mandibular length.

**23** Lower tooth of mandible: tip 33/87

(0) coming to a sharp point (Figs. 29, 69)

(1) slightly to strongly rounded (Fig. 76)

Slight intraspecific variation exists in the shape of the tip of the lower mandibular tooth; such variation is greatest in those taxa with a “rounded” state (1). Based on the presence of taxa in which the lower mandibular tooth comes to a distinct sharp point, it was concluded that the prominently blunt, or rounded mandibular tooth is not a result of environmental wear and tear.

**24** Lower tooth of mandible: shape 100/100

(0) Smooth, not distinctly separated into upper and lower areas (Figs. 22, 76)

(1) An upper and a lower area can be distinguished by the presence of an indistinct crease, lower area usually extending beyond the upper (Figs. 69, 72)

The crease described in character state (1) is not very distinct in some taxa. The two areas in question may be differentiated by the distinctly truncate nature of the mandibular tooth, the lower part of which usually extends beyond the upper.

**2** Epistomal suture 50/83

(0) more or less distinct, not very prominent (Figs. 22, 25)

(1) entirely absent (Figs 69, 72)

(2) prominent (Figs 42, 50)

The depth of the epistomal suture is a subtle character, whereas its absence is quite easily observed and scored. Character states 0 and 2 can sometimes exhibit a continuous nature in some intermediate species, while being quite distinct in taxa with a protruding clypeus.

**4** Face: surface 66/88

(0) completely flat (Figs. 42, 69)

(1) slightly raised medially, slightly concave laterally (Figs. 22, 76)

(2) bulging medially (Figs. 38, 56)

(3) bulging dorsally, concave ventrally (Figs. 65, 67)

(4) distinctly raised, to slightly bulging medially, concave laterally (Figs. 10, 63)

The contours of the face vary distinctly among taxa, this difference is especially pronounced among genera of Scolobatini (character states 2-4), whereas other taxa have fairly uniform facial features.

**6** Face: morphometrics 25/70

(0) less than 1.5 times as broad as long

(1) greater than 1.5 times as broad as long

Face length is measured from the anterior-most margin of toruli to the dorsal-most margin of antennal tentorial pits. Face width is measured at shortest distance between eye margins.

**9** Apical tooth on face 100/100

(0) absent

(1) present

The morphological feature in this character is situated slightly ventral to the mid-point between toruli. It is present in many taxa outside the ones examined here, and as its reduction is more commonly observed in the more derived groups, it can be hypothesized that such is the derived condition.

**8** Interantennal and postantennal areas 100/100

(0) smooth, or with a very indistinct medial longitudinal crease (Figs. 54, 61)

(1) with a prominent median longitudinal ridge (Figs. 76, 80)

The two states of this character delineate two distinct morpho-groups. No intermediates have been observed.

**5** Occipital carina 50/66

(0) present, but vestigial, not reaching beyond ventral 0.2 of occiput

(1) present, prominent, but distinctly incomplete dorsally

(2) present, complete

The extent of development of the occipital carina varies widely among taxa. Character states 1 and 2 represent two stages of a continuous series of carinal reduction. This character has much phylogenetic information for species-level classification.

**0** Occipital and hypostomal carinae 66/75

(0) do not join at mandibular base, both reaching mandible (Fig. 91)

(1) join at mandibular base

(2) join before mandibular base (Fig. 83)

Joining point of the occipital and the hypostomal carinae can be difficult to observe due to the head positioning of some specimens, but is distinctly visible once the head is detached from the body. SEM images were taken of a few *Physotarsus* species in which the two carinae parallel each other very closely without joining at or before the mandibular base.

### *Prothorax*

**25** Lateral corner of pronotum above prothoracic spiracle 100/100

(0) not extended, triangular

(1) narrowly extended and downturned laterad

Character state (1) is an unusual and quite distinct modification found in a few of the examined taxa.

**27** Lateral longitudinal groove of the pronotum 50/90

(0) extending past dorsal 0.4 of the pronotum

(1) reaching dorsal 0.4 of the pronotum, or terminating prior to that

The lateral longitudinal groove of the pronotum is present dorsally as a crease in all taxa. Its lateral presence and termination point vary widely, both aspects sometimes associated with the texture of the pronotum. Although this character is continuous, it is not subdivided into any further character states due to occasional interspecific variation in the termination point of the lateral groove of the pronotum.

### *Mesothorax*

**26** Epicnemial carina 100/100

(0) largely parallel to anterior margin of mesopleuron (Fig. 92)

(1) strongly angled towards the anterior margin of mesopleuron (Fig. 93).

The epicnemial carina never reaches the anterior margin of the mesopleuron in those taxa.

**19** Propodeum: lateral texture 60/86

(0) lightly to moderately punctured, pubescence absent entirely or very indistinct

(1) punctures absent entirely or indistinct, pubescence quite prominent

(2) surface quite smooth, punctures and pubescence very indistinct

(3) surface strongly punctate to coarse, pubescence variable

The main focus of this character is the punctation, characteristics of the pubescence are included to provide a more complete description of the usual condition. The amount of pubescence varies intraspecifically in some species, thus not allowing for delineation of a separate character.

**20** Propodeum: posterolateral corner/edge 66/66

(0) regularly rounded or sub-truncate, flat, not protruding

(1) somewhat upcurved

(2) protruding outwards and quite strongly flanged

The posterolateral edge of the propodeum, if not distinctly delineated as in character state (2), is defined as the posterior-most 1/3 of the lateral margin of the propodeum. As the posterior lateral margin of some taxa is rounded, it is coded based on its level of outwards projection.

**3** Propodeum: median longitudinal carina 40/72

(0) entirely absent

(1) vestigial, not reaching the anterior 0.5 of the propodeum

(2) prominent, reaching at least the anterior 0.5 of the propodeum

Vestiges of the lateral longitudinal carina are also evident in some species, however, their presence and extent are quite irregular.

*Legs***14** Trochanter 100/100

(0) less than 3.0 times as long as wide basally

(1) more than 4.0 times as long as wide basally

The distinction between these two states is quite evident, state (1) is only present in one genus.

**15** Trochanter and trochantellus 100/100

(0) apical extension of trochanter reaching the apical margin of trochantellus, which appears cleft

(1) apical extension of trochanter not reaching the apical margin of trochantellus.

This condition commonly occurs on the posterior side of leg, although in some cases the leg is twisted in its socket.

**16** Hind leg: the longest tibial spur 100/100

(0) less than or equal to 0.3 times the length of tarsomere 1

(1) longer than 0.3, but less than 0.65 times the length of tarsomere 1

(2) longer or equal to 0.65 times the length of tarsomere 1

The tibia usually terminates with two distinct tibial spurs, one of which is significantly longer than the other. This character is continuous, and refers to the farthest reach of a tibial spur along tarsomere 1.

**17** Hind leg: pretarsus and tarsomere 3 50/71

(0) pretarsus not as long as tarsomere 3

(1) pretarsus equal in length to tarsomere 3

(2) pretarsus longer than tarsomere 3

**18** Hind leg: pretarsus and tarsomere 4 100/100

(0) pretarsus longer than tarsomere 4

(1) pretarsus equal in length to tarsomere 4

Tarsomeres 3 and 4 exhibit great degree of variation in length among taxa, whereas the pretarsus length is relatively quite stable.

**7** Claws 66/85

(0) simple, pectination entirely absent

(1) basally pectinate, serration reaching at most 2/3 of total claw length

(2) 3/4 to fully pectinate (Fig. 94)

Upon close examination, the teeth on the claws have been found to be covered in small longitudinal ridges (Fig. 94, *P. maculipennis*). Unfortunately,



this character seems universal in all taxa examined in this study. It is possible, however, that variation is present among other more distant taxa.

### *Wings*

#### **12** Forewing vein Rs+2r 100/100

(0) originating at mid-pterostigma (Fig. 95)

(1) originating at or near proximal end of pterostigma (Fig. 96)

Character state (1) is an uncommon condition among ctenopelmatines, it could be related to the physical size of some species.

#### **1** Hind wing: distal abscissa of 1A (tubular) 100/100

(0) entirely absent

(1) vestigial but discernibly present as a stub

(2) quite well developed, not reaching wing margin

(3) extending to the wing margin (Fig. 96)

Tubular condition is implied in the descriptions of these character states; spectral vestige is sometimes distinct, depending on the wing color and texture

#### **22** Hind wing: distal abscissa of cubitella 37/70

(0) entirely absent

(1) vestigial, reaching up to 1/3 distance to wing margin as a tubular vein

(2) reaching up to 1/2 distance or more to wing margin as a tubular vein, not reaching margin as a tubular vein

(3) complete, reaching the wing margin as a tubular vein

The distal abscissa of the cubitella reaches the wing margin in most taxa.

*Metathorax*

**10** Tergite 1: spiracles 20/66

(0) flat

(1) distinctly raised

Spiracles of the 1<sup>st</sup> tergite are commonly somewhat raised in the tropical species, an effect probably due to an increase in the internal chamber that controls the air inflow.

**28** Cerci: site of origin 100/100

(0) originate dorsal to the middle of terminalia

(1) originate ventral to the middle of terminalia

Terminalia is defined as the terminal end of the abdomen, which is semi-truncate in form. This character is also quite prominent with no taxa examined having the point of cercal attachment being mid-way on the terminalia.

**Analyses: results and discussion**

Strict consensus topology of 2 most parsimonious trees obtained in “Win Clada” (L=87) is presented in Table 5, and the two alternative topologies (L=88) are presented in Tables 3 and 4.

*Scolobates and Onarion*

These two genera are very similar morphologically, and appear as sister taxa in

the strict consensus topology (Table 5). The branch containing *Onarion* and *Scolobates* is supported by 2 synapomorphies: the presence of a median tooth on clypeal margin (character # 13), and the shape of lower mandibular tooth, which is distinctly separated in to an upper "blunt" area and a lower extended tooth (character # 24). One of the differences between the two genera is the lighter yellowish-black coloration of the *Onarion* species, whereas most species of *Scolobates* are dark.

*Onarion* is most readily characterized by the presence of haustellate mouthparts, which also resulted in the elongate nature of the lower face, a biological adaptation for flower feeding. Only two species of *Onarion* have currently been described, although a cryptic species complex is suspected due to the variation in the size of the *O. plaumanni* specimens and the wide geographic distribution of the species. *Scolobates* is a large genus restricted mostly to the Old World, although one species is widely distributed throughout Canada and the US. The monophyly of *Scolobates* is supported by the following diagnostic characters: the presence of a basally wide triangular mandible narrowing at apex (character # 21), and hind wing abscissa of vein 1A quite well developed (character # 1). The robust mandibles is a morphological adaptation that may aid these animals in chewing their way out of 3 layers of cocoon tissue: a double-layered sawfly cocoon, as well as the cocoon spun by the parasitoid (Wharton, personal communication).

The sister group relationship of *Onarion* and *Scolobates* in the cladistic analysis leaves little room for speculation as to the speciation patterns within this clade, but leaves an interesting biogeographical problem. Genus *Scolobates* contains 12 described species, and is widely distributed in the Palearctic and Oriental region, as well as in North America and Canada. Genus *Onarion*, on the other hand, contains only 2 described species, and there exists a fairly sizeable gap between the northern-most distribution record for *Onarion* – Northern Panama, and the official southern-most record for *Scolobates* – College Station, TX. Future collections data may recover an overlap in the distribution of these two genera, shedding more light on their speciation patterns.

#### *Physotarsus and Catucaba*

The *Catucaba-Physotarsus* clade is supported by three unambiguous

synapomorphies: the distal abscissa of hind wing vein 1A is entirely absent, the median longitudinal carina of the propodeum is entirely absent, and the mandible tapering 1/3 to 1/2 ways basally with sides almost parallel at apex. *Catucaba* is a highly derived offshoot of *Physotarsus*, supported by 7 unambiguous synapomorphies. It seems to have derived from a Brazilian *Physotarsus* species group, a clade supported by a single autapomorphy: the shape of epicnemial carina, which appears strongly turned towards the anterior margin of mesopleuron, almost reaching it. SEM images of the *Catucaba* epicnemial carina and the anterior margin of mesopleuron juncture were taken in order to determine the exact termination point of the epicnemial carina (as it is very difficult to distinguish using light microscopy) (Fig. 93). In lieu of such strong support for the *Catucaba* clade, it is treated as a distinct genus, leaving the rest of *Physotarsus* paraphyletic. This treatment is also attributed to the great number of undescribed *Physotarsus* species, the addition of which to the analysis should provide more resolution to this clade.

The most distinct clade of *Physotarsus* is supported by two unambiguous synapomorphies, lateral longitudinal groove extending past dorsal 0.4 of the pronotum (CI = 50), and lateral texture of the propodeum lightly to moderately punctured, pubescence absent or indistinct (CI=60). This clade includes 12 species (Table 5), and the internal structure of this group is not very well resolved. Due to its weak support, this clade does not represent a separate genus, but rather a species group. With the exclusion of *P. laucos*, *P. niveus*, *P. albus* and *P. glabellus*, the rest of the *Physotarsus* topology is a grade rather than a distinct clade. Given the large number of undescribed species in this genus (over 20 morpho-species represented by a single specimen), the internal structure of this group remains largely unresolved.

#### *Physotarsus fabioi* Gauld, 1997

*Physotarsus fabioi* was not included in the phylogenetic analysis due to the nature of its unusual and highly autapomorphic characters. The inclusion of this taxon in the phylogenetic analysis would add to the homoplasy. The removal of *Physotarsus fabioi* from the genus *Physotarsus* is justified based on the long abscissa of 1a vein in the hind wing, as well as a number of characters which are not present in *Physotarsus* (or any of the Scolobatini genera): fore wing with abscissa of Cul between 1m-cu and Cul a 1.8

times as long as Cu1b, the lack of a tyloid on flagellomere 1, the complete lack of epicnemial and occipital carinae, propodeum with no vestiges of pleural carina, tergite 1 is 0.9 times as long as posteriorly broad, as well as a large dorso-ventrally flattened abdomen.

The type specimen of *P. fabioi* exhibits an abrupt narrowing of the ovipositor towards the tip, but it is impossible to see whether or not an ovipositor notch is present due to the way it is dried. No lateral longitudinal carinae are present on T2, thus excluding its placement into the Ctenopelmatinae, and the short length of the ovipositor excludes it from the Olethrodolini. Ovipositor shape character suggests the placement of the type specimen of *Physotarsus fabioi* in the tribe Pionini of the Ctenopelmatinae.

## CHAPTER VI

### PHYLOGENETIC ANALYSES OF SCOLOBATINI

#### Included taxa

All terminal taxa represent species. Selected species of the New World Scolobatini (sensu stricto) are included to adequately represent taxon diversity; all Australian Scolobatini are also included in this analysis. Outgroups include representatives from 2 currently most well defined tribes of Ctenopelmatinae, as well as two subfamilies that are considered to be closely related to the ctenopelmatines: Banchinae and Tryphoninae (Gauld, personal communication).

#### *List of taxa included in the phylogenetic analysis of scolobatine genera: Part 1*

1. *Catucaba anatterae* Graf, Cumagai & Dutra, 1991
2. *Catucaba montanica* Zhaurova, 2006
3. *Dictyopheltes robustus* Gauld, 1984
4. *Eclytus ornatus* Holmgren, 1857 (Tryphoninae)
5. *Euryproctus species 1* (Euryproctini, Ctenopelmatinae)
6. *Glypta virginiensis* Cresson, 1870 (Banchinae)
7. *Hypopheltes pergae* Cushman, 1924
8. *Hypopheltes species 1* (Westwoodiini, Ctenopelmatinae)
9. *Lathrolestes protrusus* Barron, 1994 (Perilissini, Ctenopelmatinae)
10. *Megaceria pagana* Morley, 1913 (Euryproctini, Ctenopelmatinae)
11. *Megaceria species 1* (Euryproctini, Ctenopelmatinae)
12. *Onarion masneri* Gauld, 1997
13. *Onarion plaumanni* Townes, 1970
14. *Pergaphaga nigra* Gauld, 1984
15. *Pergaphaga species 1* (Westwoodiini, Ctenopelmatinae)
16. *Perilissus townesi* Burks, 1952 (Perilissini, Ctenopelmatinae)

17. *Physotarsus albus* Zhaurova, 2006
18. *Physotarsus bonillai* Gauld, 1997
19. *Physotarsus varicornis* Cameron, 1886
20. *Physotarsus flavipennis* Zhaurova, 2006
21. *Physotarsus laucos* Zhaurova, 2006
22. *Physotarsus luteus* Zhaurova, 2006
23. *Physotarsus maculipennis* (Cresson, 1874)
24. *Physotarsus oculatus* Zhaurova, 2006
25. *Physotarsus tonicus* Zhaurova, 2006
26. *Scolobates auriculatus* Fabricius, 1804
27. *Scolobates longicornis* Gravenhorst, 1829
28. *Scolobates species 1* (Japan)
29. *Scolobates species 3* (Turkey)
30. *Tasmabates capitatus* Gauld, 1984
31. *Westwoodia ruficeps* Brullè, 1846

## Characters

### *Character treatment and character state coding*

Characters and matrices were compiled using the database system created and maintained by Matt Yoder and Krishna Dole (<http://peet.tamu.edu>). A total of 25 characters and 31 OTUs were used in the generic analyses, which were conducted using “WinClada” software. Characters were treated as unordered, and no character weighting was employed. No ambiguities were encountered, thus only one character state was coded for each cell in the matrix.

Unlike the previous species-level phylogeny, characters defined here have a particular emphasis on capturing wide morphological variation, as these are used to produce a phylogeny of generic relationships. As such, some of them are quite lengthy and complex. Additionally, coding was performed using 2-5 specimens, although in most cases all available specimens were utilized as only one or few were available. The use of such few specimens may inadequately represent the full extent of diversity within a

taxon, however, character definitions presented here partially account for such inadequacy.

### *Presentation format*

Characters are organized in morphological categories: Head, thorax (including legs), wings, and metathorax. Preceding each character is the character number in bold, which corresponds to the number in topologies (Tables 3-5). Following each character in parentheses is the Consistency index (CI) and the Retention index (RI) scores, presented as such: 50/75, where 50 is the CI, and 75 is the RI. After the character states follow some remarks regarding the character/character state definition, overall character utility, as well as the variation among and within character states in taxa used in these analyses.

### *Head*

#### **14** Clypeal margin: shape 66/81

(0) thin or slightly thickened, homogenous (Fig. 65)

(1) thin laterally, thickened medially (Fig. 5)

(2) distinctly protruding medially as a square lobe (constricted at base) (Fig. 7)

(3) with a median tooth (Fig. 8)

The constriction at the base of median clypeal protrusion noted in character state 2 is quite distinct and well defined. Characters of the clypeal margin have a long-standing history of utilization in species and genus-level taxonomy, with some of the included taxa being previously defined solely based on the presence or absence of a “clypeal tooth”.

#### **12** Mouthparts 100/100

(0) not haustellate (Fig. 82)



(1) haustellate (Fig. 70)

The term “haustellate” is used here to indicate the extensive mouthpart modifications observed in some taxa that are suspected to be flower feeding as adults. These modifications include an elongation of labium and maxillae (Fig. 70).

## 2 Epistomal suture 50/85

(0): more or less distinct, not very prominent (Figs. 22, 25)

(1): entirely absent (Figs. 69, 72)

(2): prominent (Figs. 42, 50)

The depth of the epistomal suture is a subtle character, whereas its absence is quite prominent. Character states 0 and 2 can sometimes exhibit a continuous nature, while being quite distinct in taxa with a protruding clypeus.

## 3 Face surface 66/83

(0) completely flat (Figs. 42, 69)

(1) slightly raised medially, slightly concave laterally (Figs. 22, 76)

(2) bulging medially (Figs. 38, 56)

(3) bulging dorsally, concave ventrally (Figs. 65, 67)

(4) distinctly raised, to slightly bulging medially, concave laterally (Figs. 10, 63)

Face surface is shaped distinctly different among taxa, this difference is especially pronounced among groups of Scolobatini (character states 2-4), whereas other taxa have fairly uniform facial features.

## 6 Median tooth on face 20/42

(0) absent

(1) present

The facial tooth is situated slightly ventral to the mid-way between toruli. It is present in many taxa outside the ones examined here, and as its reduction is more commonly observed in the more derived groups, it can be hypothesized that such is the derived condition.

**5** Area between and behind antennae 100/100

(0) smooth, or with a very indistinct medial longitudinal crease (Figs. 54, 61)

(1) with a prominent median longitudinal ridge (Figs. 76, 80)

The two states presented in this character are distinctly different from each other, thus delineating two distinct morpho-groups. No intermediates have been observed.

**16** Occipital carina 100/100

(0) entirely absent

(1) present, widely incomplete dorsally

(2) complete

(3) almost complete, narrowly obsolete dorsally

The extent of development of the occipital carina varies widely among taxa. Character states 1 and 3 represent two stages of a continuous series of carinal reduction, a character with much phylogenetic information for species-level classification.

**0** Occipital and hypostomal carinae 60/85

(0) do not join at mandibular base, both reaching mandible (Fig. 91)

(1) join at mandibular base

(2) join before mandibular base (Fig. 83)

(3) occipital carina absent entirely

Character state 3 is an autapomorphy coded for genus *Tasmabates*

**8** Tyloid on the lateral side of flagellomere 1 50/75

(0) absent

(1) present (Figs 84: Westwoodiini, Figs. 85, 86: Scolobatini)

Tyloid is a sensory patch of embedded sensillae arranged in a circular pattern in larger Australian taxa. The number of these sensillae varies proportionally to the individuals' size. Larger-sized species also tend to have shorter and "stubbier" sensillae, whereas smaller-sized species have a few elongated ones.

*Thorax*

**13** Transverse carinae of the propodeum 50/75

(0) entirely absent

(1) present anteriorly: costula and/or basal transverse carina

(2) present posteriorly: apical transverse and/or median longitudinal carina

(3) present both anteriorly and posteriorly

(4) propodeum reticulate

Carination of the propodeum varies widely among genera and species. Treatment of all components of an anterior or posterior “transverse carina” as one unit allowed for clear delineation of taxa in to groups, rather than using multiple complex autapomorphic characters.

**9** Notauli 50/81

(0) absent

(1) present, reaching up to the anterior half of the mesoscutum

(2) present, reaching 3/4 to the posterior margin of the mesoscutum

Depth of notauli is also a variable character, but is not used in this analysis. Most taxa in which notauli are present have them very prominent and quite deep.

**15** Foretibial tooth 100/100

(0) absent

(1) present

A tooth on the anterior edge of foretibia is one of the defining characters for the subfamily Ctenopelmatinae.

**4** Claws: interior surface 50/85

(0) simple (no serration)

(1) basally pectinate

(2) almost (3/4) to fully pectinate (Fig. 94)

The extent of claw pectination varies widely among species, whereas “simple” claws, or those lacking serration entirely, are characteristic of the endemic Australian taxa represented in this study.

### *Wings*

#### **10** Areolet in forewing – vein 3rs-m 50/90

(0) closed, vein 3rs-m present (Fig. 96)

(1) open, vein 3rs-m absent (Fig. 95)

The areolet may also be petiolate: veins 3rs-m and 2rs-m joining before reaching vein Rs anteriorly. This condition, however, is not specific to any single taxon, but occurs as a polymorphism within some taxa.

#### **20** Forewing veins cu-1 and cu-a 50/81

(0) veins equal in length

(1) cu-1 shorter than cu-a

(2) cu-1 longer than cu-a

Character states are very distinct in this character.

#### **17** Forewing vein Rs+2r 100/100

(0) originating at mid-pterostigma (Fig. 95)

(1) originating at or near proximal end of pterostigma (Fig. 96)

Character state 1 is an uncommon condition among Ctenopelmatinae, it could be related to the physical size of some species.

#### **1** Hind wing: distal abscissa of 1A (tubular) 60/88

- (0) entirely absent
- (1) vestigial but discernibly present as a stub
- (2) quite well developed, not reaching the apical margin of wing
- (3) extending to the basal margin of wing

Tubular condition of this state is implied; spectral vestige is sometimes distinct, depending on the wing color and texture.

### *Metathorax*

#### **18** Abdomen: shape 100/100

- (0) posteriorly flattened laterally
- (1) posteriorly flattened dorsoventrally

These character states may vary in how prominent they appear due to the “softer”, less sclerotized nature of the abdominal segments of some taxa.

#### **22** Glymma: shape 100/100

- (0) belonging to glymmal group 1 (Fig. 89)
- (1) belonging to glymmal group 2 (Fig. 90)
- (2) belonging to glymmal group 3 (Fig. 97)
- (3) belonging to glymmal group 4 (Fig. 98)
- (4) glymma absent entirely

The term glymma is currently broadly interpreted as a lateral concavity that originates in the anterior half of the 1<sup>st</sup> tergite. It is occasionally further

described in taxonomic works as being “deep” “well-developed”, or “shallow”, “basal” or “almost entirely” to “entirely absent”. Upon closer examination, the ichneumonid glymma appears to be a complex set of interacting characters, that go well beyond a mere “glymma present” and “glymma absent”. Like most morphological characters, the shape and sculpture of the glymma is largely based on the underlying musculature, as well as the size and point of attachment/pull of musculature of the closely-associated spiracular chamber (if one is present internally).

The petiolar connection of the propodeum and the abdomen includes two major sets of longitudinal muscles: dorsal and ventral. Those broad categories are further subdivided in to the external and the internal muscle sets, evidently referring to the relative placement of muscle fibers within the body wall (Snodgrass 1993). Not all insects have a prominent muscular connection between the 1<sup>st</sup> and the 2nd abdominal segments, but based on my dissections I conclude that ichneumonids do. This juncture is extremely important in all apocritans because it serves as the narrow connection between thorax and gaster. I can only speculate that the contraction of the dorso-median muscle would result in abdominal elevation, whereas the contraction of the ventro-median muscle would make the abdomen contract in the downward motion. A glymma, therefore, may either interrupt or provide an attachment point of dorsal and ventral longitudinal muscle groups.

“Dorsolateral carina” is the term used by Townes to describe carinae that originate just above the glymma, partially delineating it. Similarly, ventrolateral carinae serve the same purpose ventrally, and are sometimes extremely vestigial and hardly distinguishable from the tergo-sternal suture. Within the Scolobatini, dorsolateral carinae are largely very well developed, appearing as clear ridges in some taxa. It is also important to note here that sternites 2-4(5) in some taxa examined here are membranous and extremely enlarged, thus making the laterotergites indistinguishable. The glymma in such groups (*Westwoodia*, *Scolobates*, *Physotarsus*) somewhat varies in depth and length, but is distinctly

delimited distally, with a fairly distinct edge. This combination of characters is here referred to as **Glymmal Group 1** (Fig. 89). Another instance is that of the Westwoodiini genera: *Hypopheltes*, *Dictyopheltes*, and *Pergaphaga*. The latter was originally described as having no glymma at all, but upon closer examination *Pergaphaga* and the other two genera are placed in **Glymmal Group 2** (Fig. 90), based on the lack of distal delineation described in Glymmal Group 1. It is important to note the extent of variation in the depth of glymmae between *Hypopheltes* and *Pergaphaga*, with the glymma of *Dictyopheltes* resembling much closer that of *Pergaphaga*. Such variation, in my opinion, is of less phylogenetic value than the categories described above. Another very important character of the first two glymmal groups is that they both arise *before* the dorso-median tendonal juncture (defined below).

**Glymmal Group 3** (Fig. 97): is defined here as the type of glymma that arises after the dorso-median tendonal juncture, and is quite long and well delimited laterally by the dorsolateral and the ventrolateral carinae, as well as distally. This type of glymma is found in the Perilissini: *Perilissus* and *Lathrolestes*, as well as the Tryphoninae. Finally, the Banchinae, represented in the analyses by *Glypta virginiensis* Cresson, 1970, possess yet another type of glymma: it is situated largely ventrolaterally and delimited dorsally by an extensively developed and laterally protruding dorsolateral carinae. The first tergal segment is extremely wide and steeply sloped, with a pair of distinct dorsal carinae. This is here referred to as **Glymmal Group 4** (Fig. 98).

## 23 Dorsal tendon attachment on tergite 1 71/71

- (0) dorsal tendon attaches to a semi-flat surface, dorso-median tendonal juncture with circular grooves
- (1) dorso-medial tendonal juncture on tergite 1 is slightly to quite distinctly sloped
- (2) dorso-medial tendonal juncture hollow, sharply raised, sometimes curved under, dorsal tendon enters anteriorly into a deep semicircular concavity.



(3) dorso-medial tendonal juncture shallow, dorsal tendon enters in to a shallow semi-circular concavity

(4) dorso-medial tendonal juncture flat, sharply sloped.

Specimens with the first abdominal segment not pressed up against the propodeum tend to display what appears to be the propodeal-petiole juncture of the dorsal median muscle, or the **dorsal tendon**. This tendon is received in the 1<sup>st</sup> metasomal tergite by the abdominal **dorso-median tendonal juncture**, which is flat to highly elaborate, and may be of some phylogenetic significance.

# 19 Tergite 1: shape 80/87

(0) thin, elongate, sub-trapezoidal to cylindrical (Fig. 99)

(1) anterior 2/3 elongate, sides parallel, distal 1/3 significantly widened (Fig. 100)

(2) anterior 1/2 elongate, sides parallel, distal 1/2 widening, sub-trapezoidal (Fig. 101)

(3) not distinctly elongate, sides parallel or sub-trapezoidal along entire length (Fig. 102)

(4) proximal 1/4 narrow, sides parallel, distal 1/3 widening, sub-trapezoidal (Fig. 103)

# 11 Tergite 1: ventrolateral carina posterior to spiracle 50/66

(0) absent (Fig. 89)

(1) present (Fig. 98)

The ventrolateral carina on the 1<sup>st</sup> tergite is a prominent feature if present. It sometimes is a continuation of the ventrolateral carina anterior to spiracle, which delineates the glymma.

**21** Tergo-sternal juncture on the 1<sup>st</sup> abdominal segment 100/100

(0) tergite and sternite distinctly separate

(1) tergite and sternite fused

Tergo-sternal fusion produces a tubular structure at the anterior-most abdomen; tergo-sternal suture is quite distinct when present.

**7** Sternite 1: relative distal extension 66/75

(0) reaching to, or terminating before the anterior 0.6 of mid-tergum

(1) reaching 0.7-1.0 of tergum, but not beyond its posterior margin

(2) reaching beyond the posterior margin of tergum

The posterior margin of sternite 1 is usually u-shaped, with its lateral edges terminating further posteriorly. Measurements for this character were made at the shortest distance of sternite 1: along the midline.

**24** Cerci: site of origin 100/100

(0) originate dorsal to the middle of terminalia

(1) originate ventral to the middle of terminalia

This character is also quite prominent with no taxa examined having the point of cercal attachment being mid-way on the terminalia.

*Potentially useful characters not included in the analyses*

Some phylogenetically informative characters were omitted from the generic analysis while used in the species-level analysis in chapter V. Other characters, especially those not found within the Westwoodiini, were omitted entirely, as their phylogenetic information is insufficient for reconstructing genus-level phylogeny. An

example of such characters are various surface textures – punctation and pubescence, as well as minor morphometric measurements associated with ocelli and the area immediately adjacent to them. As a species-level phylogeny of Westwoodiini is not attempted in this study due to gross under representation of this diverse Australian group, the phylogenetic utility of these characters can only be hypothesized.

### **Analyses: results and discussion**

Computational methods used in this analysis are outlined in the “Phylogenetic analyses” section of Chapter II. The resulting phylogeny (Table 7) is a strict consensus of 101 most parsimonious trees (L=87). It illustrates two distinct clades: the Scolobatini (sensu novo), which includes *Catucaba*, *Onarion*, *Physotarsus* and *Scolobates*, and the Westwoodiini, which includes *Dictyopheltes*, *Hypopheltes*, *Pergaphaga* and *Westwoodia*. As such, the split of the Scolobatini (sensu Gauld, 1984) into two distinct tribes is supported by the phylogenetic analysis.

#### *Scolobatini*

The lower branch of the tree represents the new clade Scolobatini, and is very well supported by 7 characters: 3 diagnostic and 4 homoplastic. Four internal clades are present. The most distinct of these contains the genera *Onarion* and *Scolobates*; and another branch contains the 2 species of *Catucaba*. The remaining clades are those of various species groups of *Physotarsus*, discussed in detail in the previous chapter. Most of the Scolobatini clade is unresolved, however, indicating only the strong monophyly of these taxa in relation to higher-level classification. Greater resolution is provided and discussed in the species-level analysis performed with more taxa (Chapter V).

#### *Tasmabates*

The phylogenetic placement of *Tasmabates* remains a mystery, as this analysis only indicates its removal from the Scolobatini and the Westwoodiini. It is important to note, however, that the branch containing Euryproctini, Westwoodiini and the Scolobatini is weakly supported by only one character: the absence of a ventrolateral carina posterior

to the spiracles on tergite 1. This carina is present in *Tasmabates* and in one other outgroup taxon of a different subfamily (Tryphoninae: *Eclytus ornatus*). *Tasmabates* is represented by a single type specimen (male) and possesses many autapomorphies as well as a combination of characters that are novel relative to the tribes included in the analyses.

The branch containing *Tasmabates* and the Euryproctini, Westwoodiini, Scolobatini clade is supported by 3 diagnostic characters. Additionally, *Tasmabates* is the only species of Ctenopelmatinae of such small size found in Australia, suggesting distinct biological (host) differences. The notably large size of species within Westwoodiini is attributable to biological similarities: all are parasitoids of sawflies of the genera *Perga*, *Pseudoperga*, and *Pergagrapt*, which are all quite large. An extreme sexual dimorphism in size is a possibility, but no female specimen of *Tasmabates* is available.

### *Hypopheltes*

The analysis suggests that the genus *Hypopheltes* is paraphyletic. Two distinct morpho-species were used in the analysis, one of which was identified as *Hypopheltes* by Ian Gauld, and remains undescribed. Aside from variations in color and texture, the two species also exhibit great differences in the carination of the propodeum, *H. pergae* having multiple transverse carinae, and *H. species 1* lacking them entirely. This variation alone may provide sufficient grounds for the recognition of a separate genus for the taxon *H. species 1*, however, due to the lack of specimens it is not described in this work. Additional characters in support of *Hypopheltes* are presented in the morphological description of this genus in Chapter V. The small number of known taxa in the Westwoodiini makes a separate species-level analysis ineffective.

According to the strict consensus topology, *Westwoodia* is the basal-most group of the Westwoodiini, with the consecutive evolution of *Dictyopheltes*, *Hypopheltes* and *Pergaphaga*, respectively. *Pergaphaga* and *Dictyopheltes* exhibit a number of autapomorphies specific to these genera, which are not included in the analyses due to their ineffectiveness in resolving inter-generic relationships. As in the case of *Hypopheltes*, the addition of taxa would greatly improve the resolution of the Westwoodiini clade.

### *Westwoodiini and Euryproctini*

Sister group relationship between Westwoodiini and Euryproctini (*Euryproctus* and *Megaceria*) is supported by a single character, the presence of simple claws. The two tribes are distinguished from one another by a number of synapomorphies, those of the Westwoodiini being the prominent ridge between antennae, vein  $rs+2r$  of the forewing originating near proximal end of pterostigma, and an unusual site of cercal attachment ventrad to the middle of the posterior aspect of gaster. Euryproctini, in turn, is supported by 4 diagnostic synapomorphies which make it the most strongly supported tribe included in this analysis: first sternum reaching beyond mid-tergum, a laterally flattened abdomen, the absence of a glymma, and the attachment of petiolar dorsal tendon to a flat surface. In addition to the diagnostic characters discussed above, a number of other characters also support the tribe Euryproctini.

### *Perilissini*

Representatives of 2 perilissine genera were included in this analysis: *Perilissus* and *Lathrolestes*. Both are large genera with highest species richness in the Holarctic region, and are distributed world-wide (except Australia and Antarctica) (Townes 1970 b, Gauld 1997). Monophyly of the Perilissini is supported by a distinct shape of the tergite 1 (a diagnostic character), as well as forewing vein Cu-1 equal in length to vein Cu-A (a non-diagnostic character). The Perilissini is the most basal branch of the Ctenopelmatinae in this analysis. No other taxa from the tribes Mesoleiini, Pionini and Olethrodolini were included in this analysis. Further examination of relationships among the Ctenopelmatinae tribes should aid in their proper phylogenetic definition and delineation.

### *Outgroup subfamilies: Tryphoninae and Banchinae*

Higher phylogenetic relationships among ichneumonid subfamilies are debated, although it has been suggested that Banchinae, Tryphoninae, and Ctenopelmatinae form the basal clade within the "Ophioniformes" (Gauld 1988, Wahl 1991), hence the choice of one species of Banchinae and Tryphoninae as outgroups. Banchines are known to

attack larvae of Lepidoptera, whereas tryphonines attack both Lepidoptera and Tenthredinidae. The genus *Eclytus* (Tryphoninae: Eclytini) was chosen due to its similarity to the Ctenopelmatinae in their tenthredinid host preferences (Gupta 1988). Tryphonines are a very morphologically diverse group, overlapping frequently with some Ctenopelmatinae. The monophyly of tryphonines is currently supported solely by their stalked egg morphology (Bennett 2002).

### *Ctenopelmatinae*

This subfamily of Ichneumonidae is currently supported by the presence of a fore tibial tooth and a biological trait of parasitism of Symphyta. The fore tibial tooth is also present in the subfamily Mesochorinae (Gauld and Wahl 2006), and the parasitism of Symphyta “may be a plesiomorphy of the Ophioniformes (Gauld and Wahl 2006, Gauld 1988). As such, Ctenopelmatinae are probably not monophyletic. Recent molecular and morphological works suggest Ctenopelmatinae to be paraphyletic with respect to the Mesochorinae (Belshaw and Quicke 2002), and the Metopiinae (Belshaw and Quicke 2002, Gauld and Wahl 2006).

### *Physotarsus fabioi* Gauld 1997

The removal of this taxon from the Scolobatini is based on the combination of the following characters: fore wing with abscissa of Cu1 between 1m-cu and Cu1a 1.8 times as long as Cu1b, the lack of a tyloid on flagellomere 1, the complete lack of epicnemial and occipital carinae, propodeum with no vestiges of pleural carina, tergite one 0.9 times as long as posteriorly broad, and the presence of a large dorso-ventrally flattened abdomen.

The suggested placement of this taxon is within the tribe Pionini, however, the current preservation of the ovipositor of the type specimen of *P. fabioi* makes positive determination difficult. This taxon was not included in the phylogenetic analyses due to the presence of numerous autapomorphies, a situation remedied by the addition of more similar taxa.

## CHAPTER VII

### CONCLUSION

This work consists of a taxonomic and phylogenetic revision of *Physotarsus* (Ichneumonidae: Ctenopelmatinae: Scolobatini), and phylogenetic analysis of genera previously included in the tribe Scolobatini (Hymenoptera: Ichneumonidae: Ctenopelmatinae). The revision of *Physotarsus* resulted in the removal of one species, *P. fabioi* Gauld, 1997, from the genus, as well as description of 17 new species. *P. davidi* is treated as a junior subjective synonym of *Scolobates varicornis*, the name *Physotarsus varicornis* is retained. A key to all but one *Physotarsus* species (*P. motnezuma*) is produced.

Phylogenetic analysis demonstrates the relationship among species of *Physotarsus*, as well as genera within the Scolobatini (sensu novo). Of the 4 Scolobatini genera, *Onarion* and *Scolobates* are monophyletic sister groups, whereas the genus *Physotarsus* appears to be paraphyletic in relation to *Catucaba*. Based on phylogenetic analysis, the Scolobatini (sensu Gauld, 1984) is split into two tribes: the Scolobatini (sensu novo), redefined to include the genera *Catucaba*, *Onarion*, *Physotarsus* and *Scolobates*, as well as the Westwoodiini, resurrected and defined to include the genera *Dictyopheltes*, *Hypopheltes*, *Pergaphaga* and *Westwoodia*. Tribes Westwoodiini and Euryproctini appear as sister groups in the analysis. Comparative species descriptions are provided for *Physotarsus* and *Catucaba*, and comparative generic descriptions are provided for all genera of Scolobatini and Westwoodiini.

Future work on taxa of Scolobatini should focus on revising the genus *Scolobates*, as its relationship to other scolobatine genera is imperative to the understanding of the internal classification of this tribe. A better understanding of the taxonomic status and the phylogenetic relationships of other Ctenopelmatinae genera and tribes is also required to resolve the placement of Scolobatini and Westwoodiini within the subfamily. Both of these tasks require the addition of more taxa. Based on the amount of apparent species diversity in these tribes, our understanding of their relationships and biology is currently minimal.

## REFERENCES

- Aubert, J. F. 1993. Ichneumonidae Scolobatinae d'un genre nouveau, *Pionpherta* genus novum (Hymenoptera, Ichneumonidae). *Nouvelle Revue d'Entomologie* 10 (4): 358.
- Barron, J. R. 1994. The Nearctic species of *Lathrolestes* (Hymenoptera: Ichneumonidae: Ctenopelmatinae). *Contributions of the American Entomological Institute* 28 (3): 135pp.
- Basibuyuk, H. H., Quicke, D. L. J. 1998. Gross morphology of multiporous plate sensilla in the Hymenoptera (Insecta). *Zoologica Scripta* 28: 51-67.
- Belshaw, R. and Quicke, D. L. J. 2002. Robustness of ancestral state estimates: evolution of life history strategy in Ichneumonid parasitoids. *Systematic Biology* 51: 450-477.
- Bennett, A. M. R. 2002. Cladistics of the Tryphoninae (Hymenoptera: Ichneumonidae) with a discussion of host use and the evolution of parasitism in the Ichneumonidae. Ph.D. Dissertation, Graduate Department of Zoology, University of Toronto, Canada 384pp.
- Brullè, M. A. 1846. Tome Quatrieme. Des Hymenopteres. Les Ichneumonides, pp. 56-324. In Lepeletier de Saint-Fargeau A. *Historie Naturelles des Insectes*. Roret Publishing, Paris. 680 pp.
- Burks, B. D. 1952. A review of the Nearctic genera of the tribe Mesoleiini with descriptions of two new genera and a revision of the Nearctic species of *Perilissus* and *Labrossyta* (Hymenoptera – Ichneumonidae). *Annals of the Entomological*



- Society of America* 45 (1): 80-103.
- Cameron, P. 1886. Insecta: Hymenoptera. Ichneumonides. *In* Godman, F. D. and Salvin O. *Biologica Centrali-Americana: Insecta, Hymenoptera*. Taylor and Francis, London 1: 241-328.
- Carlson, R. W. 1979. Family Ichneumonidae. *In* Krombein K. V., Hurd Jr. P. D., Smith D. R., and Burks, B. D. eds. *Catalog of Hymenoptera in America, North of Mexico*. Smithsonian Institution Press, Washington, DC pp. 315-740.
- Cresson, E. T. 1870. Descriptions of new species belonging to the subfamily Pimplariae found in America North of Mexico. *Transactions of the American Entomological Society* 3: 143-172.
- Cresson, E. T. 1874. Descriptions of Mexican Ichneumonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1873: 374-413.
- Cresson, E. T. 1916. The Cresson types of Hymenoptera. *Memoirs of the American Entomological Society* 1: 1-141.
- Cushman, R. A. 1924. On the genera of Ichneumon-flies of the tribe Paniscini Ashmead, with description and discussion of related genera and species. *Proceedings of the United States National Museum* 64 (2510): 1-48.
- Fabricius, J. C. 1804. *Systema Piezatorum*. Carolum Reichard, Brunsvigae, Graz, Austria. 439+32 pp.
- Gauld, I. D. 1984. *An introduction to the Ichneumonidae of Australia*. Chameleon Press Limited, London, 413 pp.
- Gauld, I. D. 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids

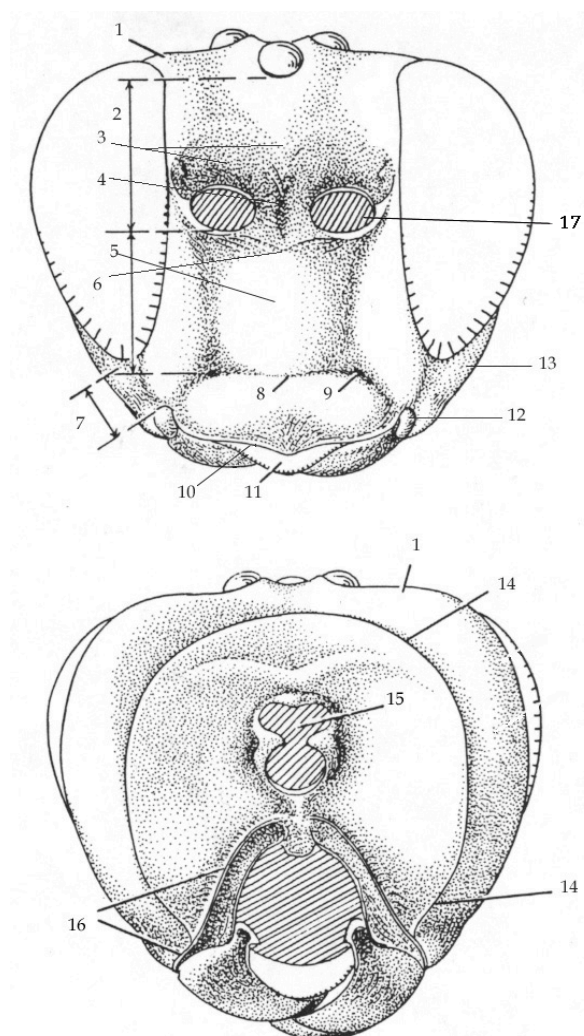
- (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society*, 35: 351-377.
- Gauld, I. D. 1991. The Ichneumonidae of Costa Rica, 1. *Memoirs of the American Entomological Institute* 47: 1-589.
- Gauld, I. D. 1997. The Ichneumonidae of Costa Rica, 2. *Memoirs of the American Entomological Institute* 57: 1-485.
- Gauld, I. D. and D. B. Wahl. 2002. The Eucerotinae: a Gondwanan origin for a cosmopolitan group of Ichneumonidae. *Journal of Natural History* 36: 2229-2248.
- Gauld, I. D. and D. B. Wahl. 2006. The relationship and taxonomic position of the genera *Apolophus* and *Scolomus* (Hymenoptera: Ichneumonidae). *Zootaxa* 1130: 35-41.
- Gokman, V. E., Krutov, V. V. 1996. On external structure of male antennae in the subfamily Ichneumonidae (Hymenoptera: Ichneumonidae) and related groups. *Zoologicheskii Zhurnal* 75: 1182-1194.
- Graf, V., A. F. Kumagai and R. R. C. Dutra. 1991. Ichneumonidae (Hymenoptera) do sul do Brasil: um novo genero de Ctenopelmatinae. *Acta Biologie Paranaense* 20 (1-4): 157-166.
- Gravenhorst, J. L. C. 1829. *Ichneumonologia Europaea. Pars II. Deliciae Musei Zoologici Vratislaviensis Fasciculus Primus*. Leopold Voss, ed., Leipzig, Germany 989 pp.
- Gupta, V. K. 1988. Relationships of the genera of the tryphonine tribe Oedemopsini and a

- revision of *Acaenitellus* Morley (Hymenoptera: Ichneumonidae: Tryphoninae). In *Advances in Parasitic Hymenoptera Research*. E. J. Brill, Leiden, pp. 243-258.
- Holmgren, A. E. 1857. Forsök till uppställning och beskrifning af de i Sverige funna tryphonider (Monographia Tryphonidum Sueciae). *Kongliga Svenska Vetenskaps-akademiens. Handlingar*, N. F. ed. 1: 93-246.
- Isidoro, N., Bin, F., Colazza, S., Vinson, S. B. 1996. Morphology of antennal gustatory sensilla and glands in some parasitoid Hymenoptera with hypothesis on their role in sex and host recognition. *Journal of Hymenoptera Research* 5: 206-239.
- Janzen, D. Biological data on *Trochophora lobata* (Erichson) (Argidae) voucher # 88-SRNP-67. Retrieved from: <http://janzen.sas.upenn.edu/Wadults/searchpara.lasso>
- Nixon, K. C. 1999-2002. WinClada ver. 1.0000 Published by the author, Ithaca, NY, USA. Retrieved from: <http://www.cladistics.com/Citations.html>
- Roman, A. 1915. Results of Dr. E. Mjöberg's Swedish scientific expedition to Australia 1910-1913. I. Schlupfwespen. *Arkiv för Zoologi*. 9(9): 1-18.
- Schmiedeknecht, O. 1911. Tryphoninae. In *Opuscula Ichneumonologica*. V. Band. (Fasc. XXIX.) Blankenburg, Germany pp. 2273-2322.
- Snodgrass, R. E. 1993. *Principles of Insect Morphology*. Cornell University Press, Ithaca, NY. 667pp.
- Townes, H. K. 1946. The generic position of the Neotropical Ichneumonidae with types in the Philadelphia and Quebec museums described by Cresson, Hooker, Norton, Provancher, and Viereck. *Boletín de Entomología Venezolana* 5:29-63.
- Townes, H. K. 1966. A catalogue and reclassification of the Neotropical Ichneumonidae.

*Memoirs of the American Entomological Institute* 8: 367 pp.

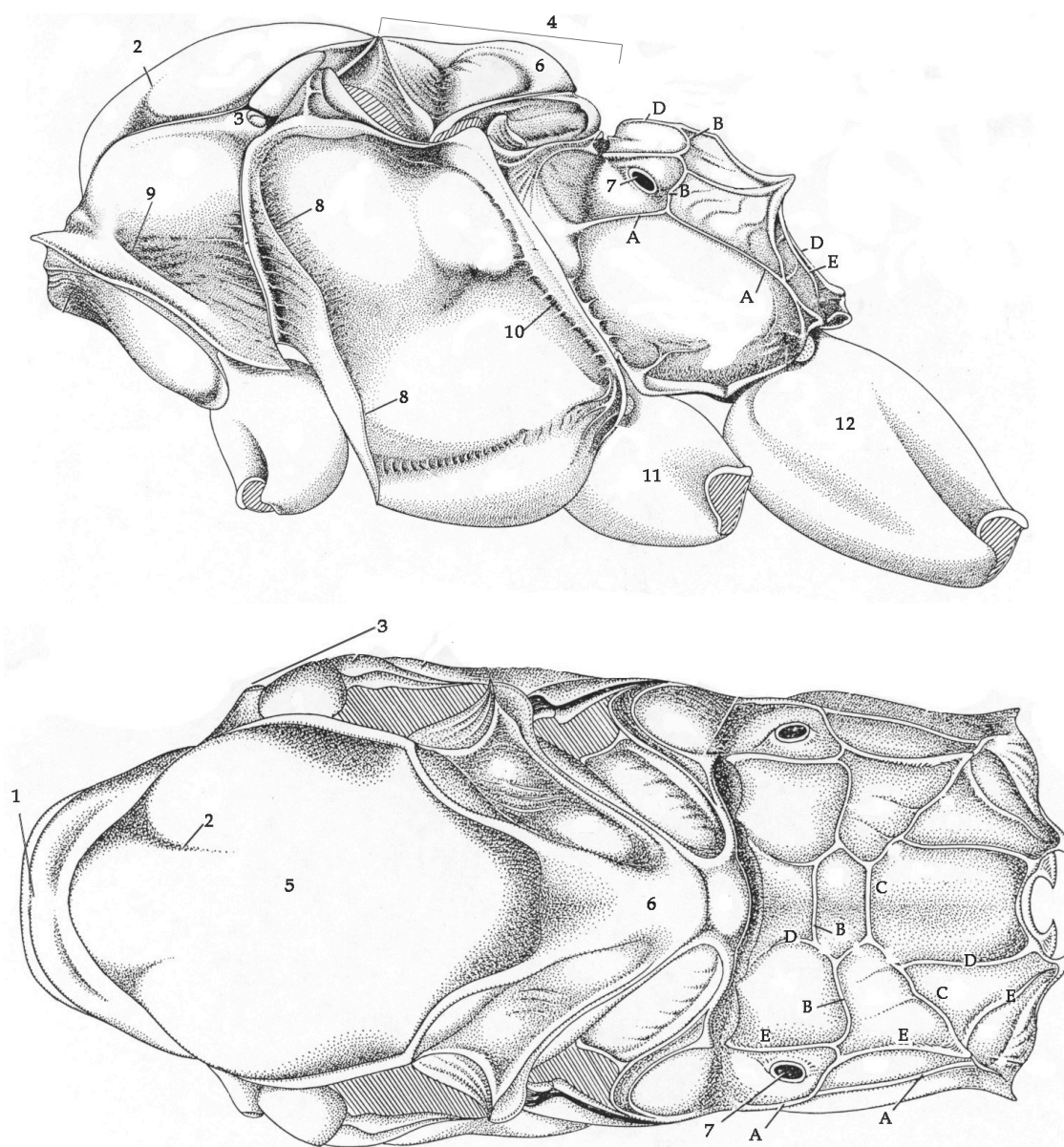
- Townes, H. K. 1969. Genera of Ichneumonidae Part I. *Memoirs of the American Entomological Institute* 11: 1-300.
- Townes, H. K. 1970a. Genera of Ichneumonidae Part II. *Memoirs of the American Entomological Institute* 12: 1-537.
- Townes, H. K. 1970b. Genera of Ichneumonidae Part III. *Memoirs of the American Entomological Institute* 13: 1-307.
- Townes, H. 1971. Genera of Ichneumonidae Part IV. *Memoirs of the American Entomological Institute* 14: 1-372.
- Townes, H. 1972. Ichneumonidae as biological control agents. *Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management* 3: 235–248.
- Wahl, D. B. 1991. The status of *Rhimphoctona*, with special reference to the higher categories within Campopleginae and the relationships to the subfamily (Hymenoptera: Ichneumonidae). *Transactions of the American Entomological Society*, 117: 193-213.
- Wenzel, J. D. 1992. Behavioral homology and phylogeny. *Annual Review of Ecology and Systematics* 23: 383-404.
- WinClada version 1.0000. 2002. Retrieved from:  
<http://www.cladistics.com/Citations.html>
- Yu, D. and K. Horstmann. 1997. Catalogue of world Ichneumonidae (Hymenoptera). *Memoirs of the American Entomological Institute* 58: 1-1558.

## APPENDIX A FIGURES AND TABLES



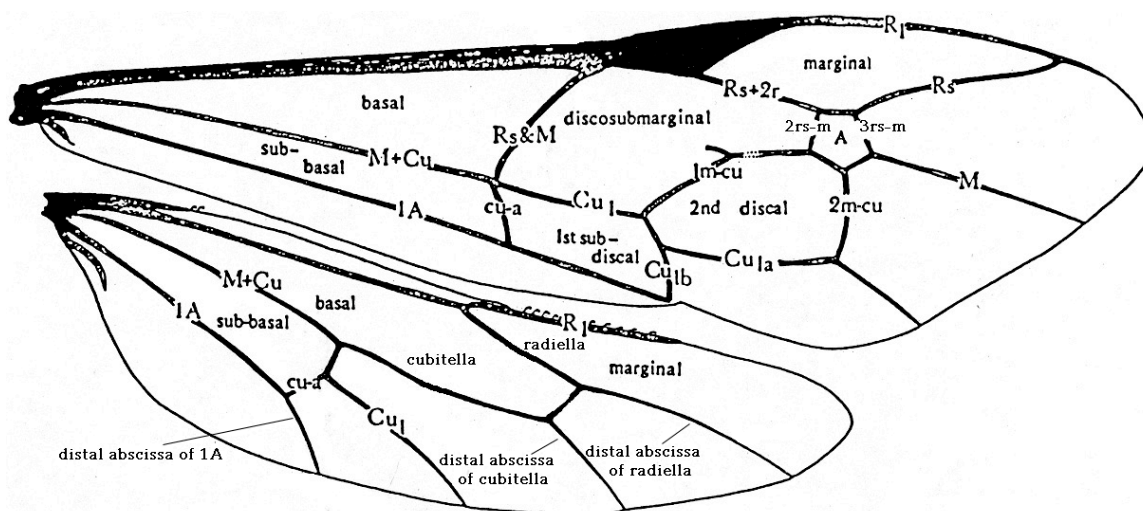
**FIG. 1:** Head of an Ichneumonid (front and rear views)

- |                                       |                           |
|---------------------------------------|---------------------------|
| 1. Vertex                             | 9. Anterior tentorial pit |
| 2. Compound eye                       | 10. Clypeal margin        |
| 3. Post-antennal area (lat. and med.) | 11. Labrum                |
| 4. Interantennal area (or ridge)      | 12. Mandibular base       |
| 5. Face                               | 13. Gena                  |
| 6. Apical tooth on face               | 14. Occipital carina      |
| 7. Malar space                        | 15. Foramen magnum        |
| 8. Epistomal suture                   | 16. Hypostomal carina     |
|                                       | 17. Torulus               |

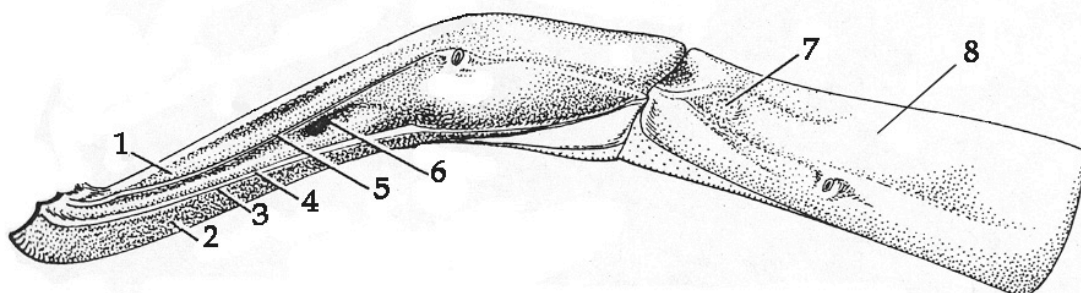


**FIG. 2:** Mesosoma of an Ichneumonid (lateral and dorsal views)

- |                               |                                |
|-------------------------------|--------------------------------|
| 1. Anterior pronotal margin   | 9. Lateral groove of pronotum  |
| 2. Notauli                    | 10. Mesopleural suture         |
| 3. Lateral corner of pronotum | 11. Mesocoxa                   |
| 4. Mesonotum                  | 12. Metacoxa                   |
| 5. Scutum                     | A. Pleural suture              |
| 6. Scutellum                  | B. Anterior transverse carina  |
| 7. Propodeal spiracle         | C. Posterior transverse carina |
| 8. Epicnemal carina           | D. Median longitudinal carina  |
|                               | E. Lateral longitudinal carina |



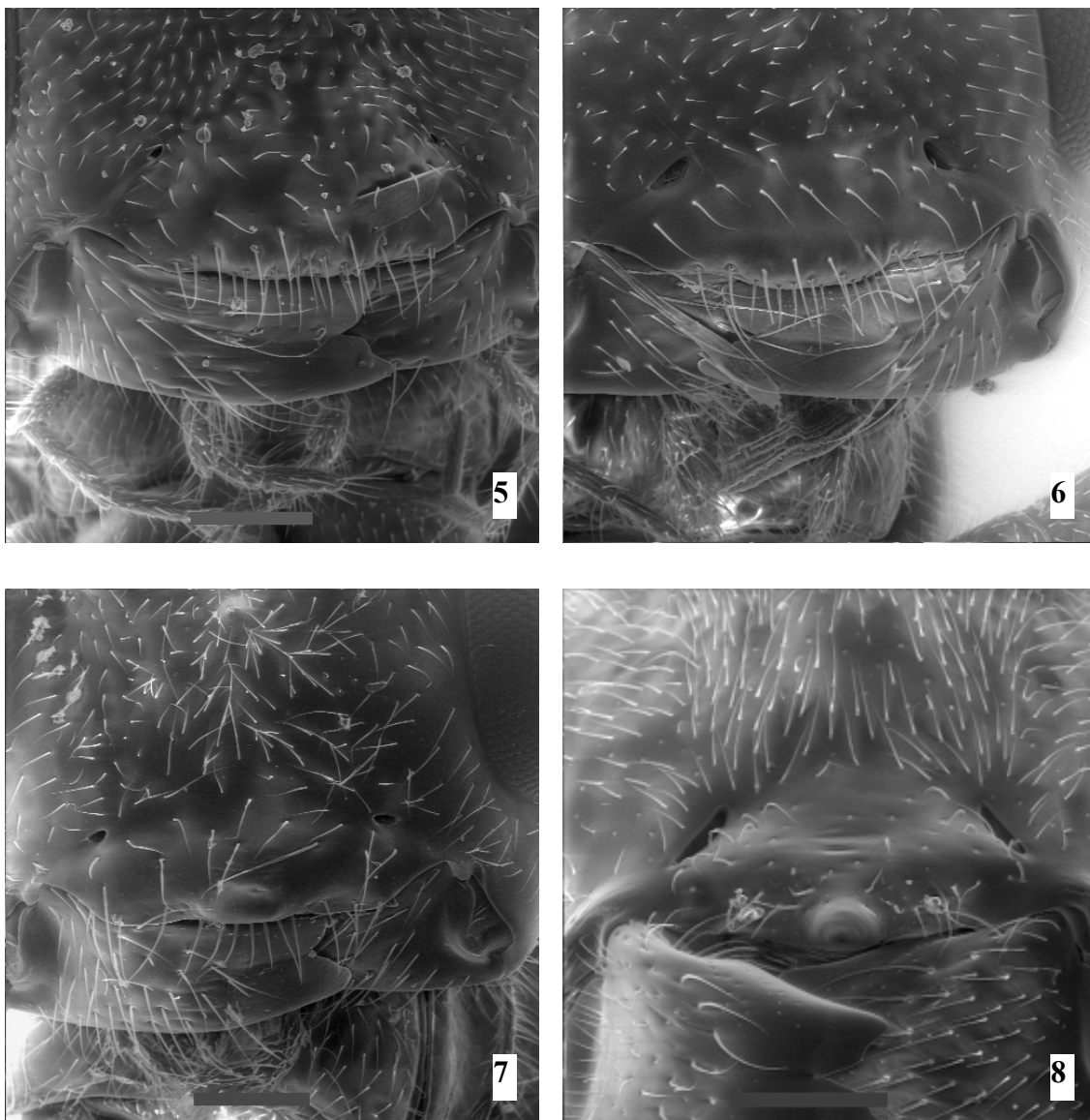
**FIG. 3:** Fore and Hind wings of an Ichneumonid  
A - areolet



**FIG. 4:** 1<sup>st</sup> and 2<sup>nd</sup> abdominal segments of an Ichneumonid (lateral view)

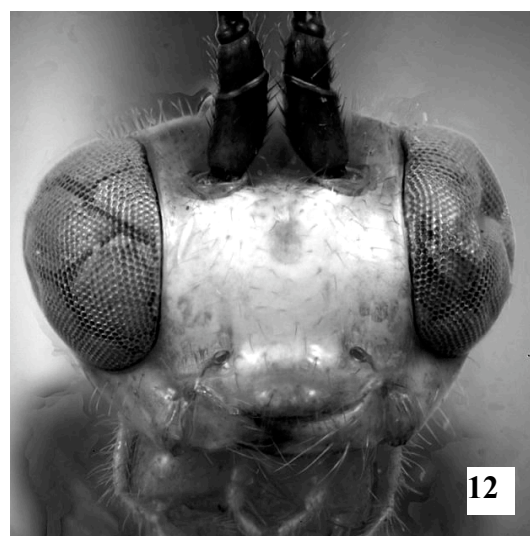
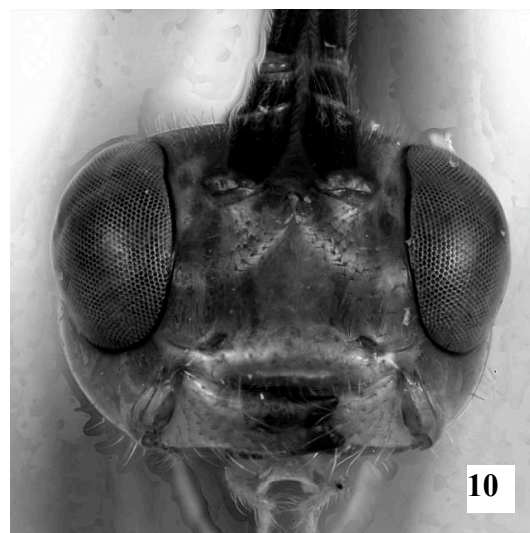
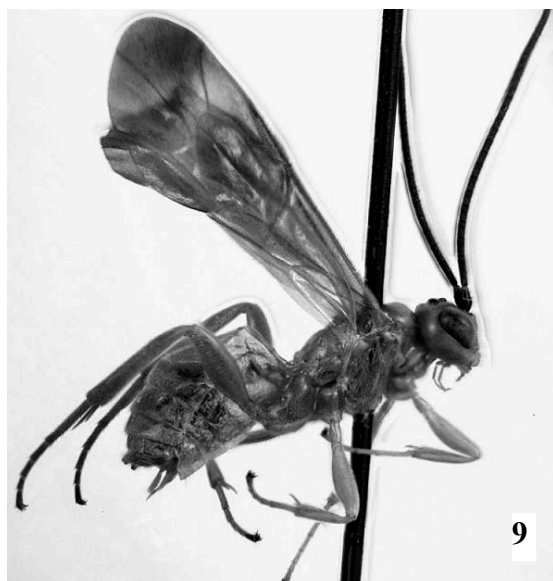
- |                          |                         |
|--------------------------|-------------------------|
| 1. Tergite 1             | 5. Dorso-lateral carina |
| 2. Sternite 1            | 6. Glymma               |
| 3. Tergo-sternal suture  | 7. Thyridium            |
| 4. Ventro-lateral carina | 8. Tergite 2            |



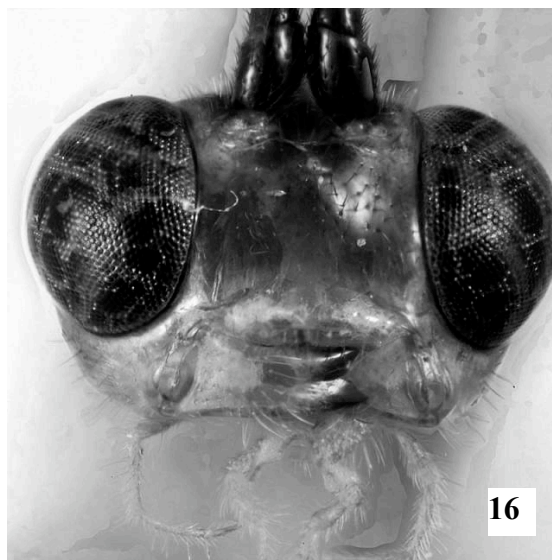
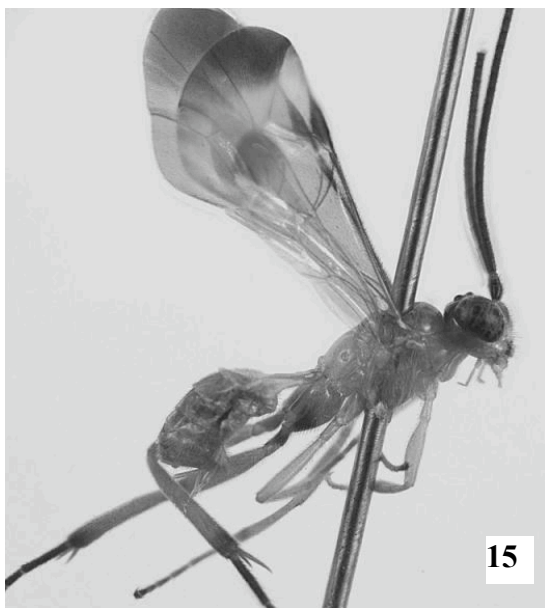
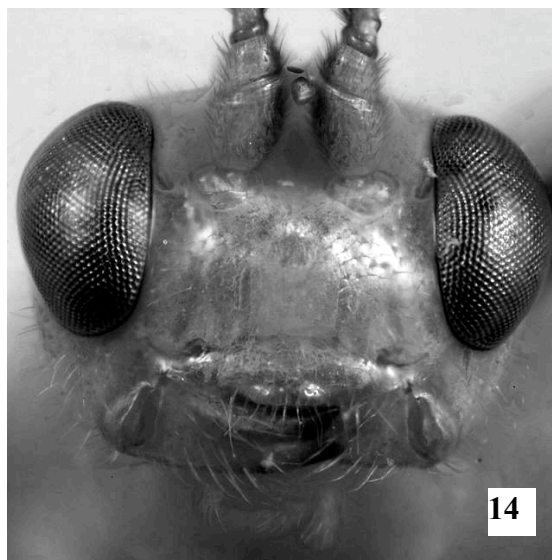
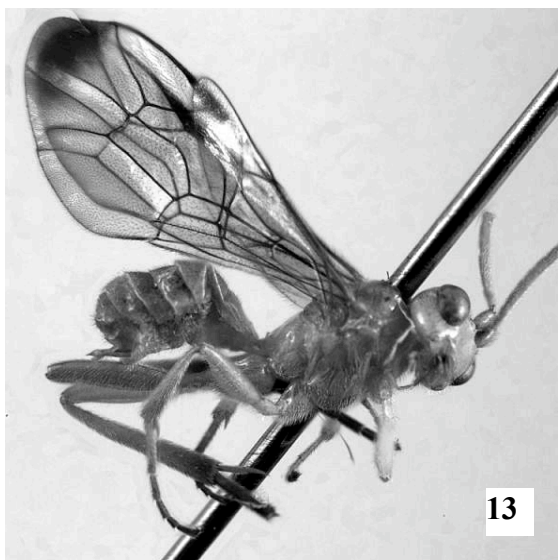


**FIG. 5:** *Physotarsus concavus* sp. nov., clypeus, **FIG. 6:** *Physotarsus luteus* sp. nov., clypeus, **FIG. 7:** *Physotarsus claviger* sp. nov., clypeus, **FIG. 8:** *Scolobates auriculatus* Fabricius, 1804, clypeus.





**FIG. 9:** *Physotarsus adriani* Gauld, 1997, habitus, **FIG. 10:** *Physotarsus adriani* Gauld, 1997, face, **FIG. 11:** *Physotarsus albus* sp. nov., habitus, **FIG. 12:** *Physotarsus albus* sp. nov., face.



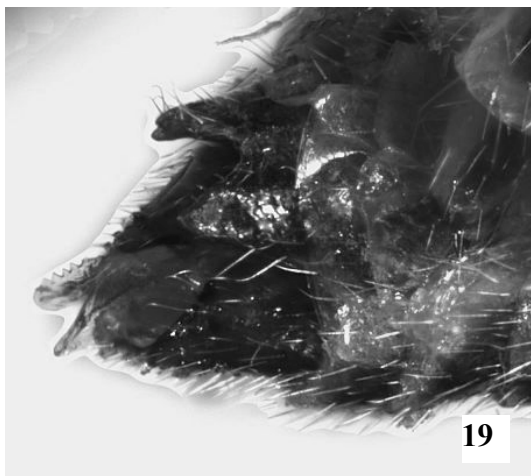
**FIG. 13:** *Physotarsus bonillai* Gauld, 1997, habitus, **FIG. 14:** *Physotarsus bonillai* Gauld, 1997, face, **FIG. 15:** *Physotarsus castilloi* Gauld, 1997, habitus, **FIG. 16:** *Physotarsus castilloi* Gauld, 1997, face.



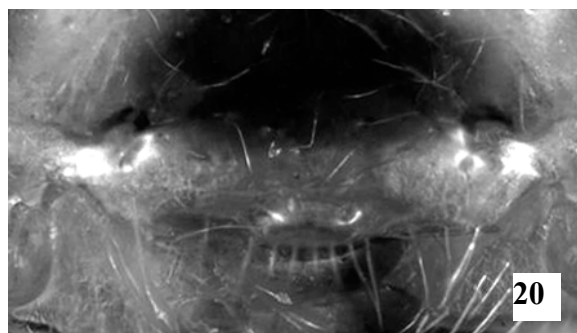
17



18



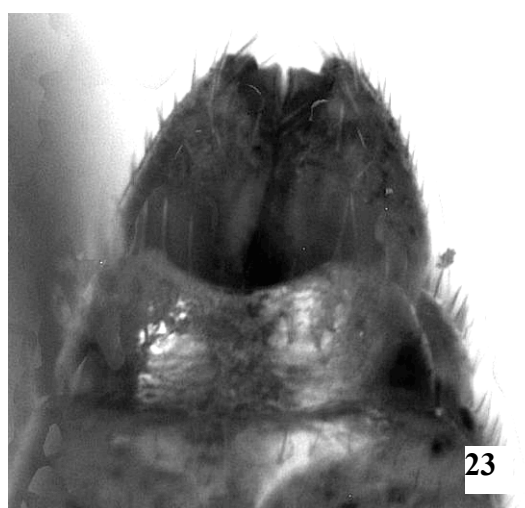
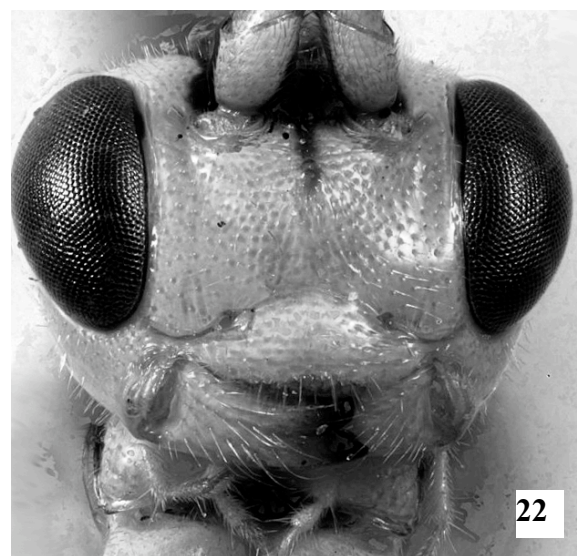
19



20

**FIG. 17:** *Physotarsus claviger* sp. nov, habitus, **FIG. 18:** *Physotarsus bonillai* Gauld, 1997, face, **FIG. 19:** *Physotarsus castilloi* Gauld, 1997, habitus, **FIG. 20:** *Physotarsus claviger* sp. nov., clypeus.

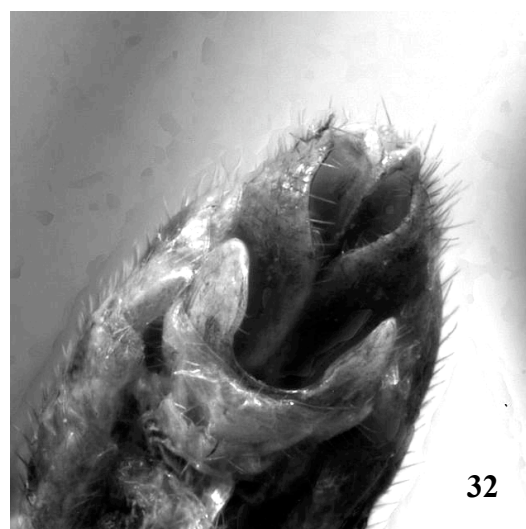
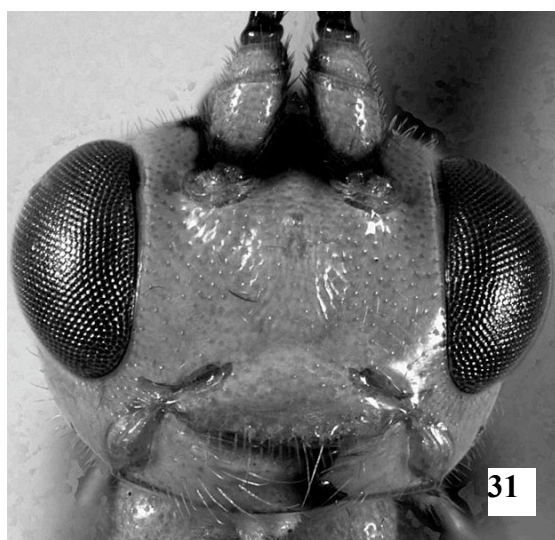
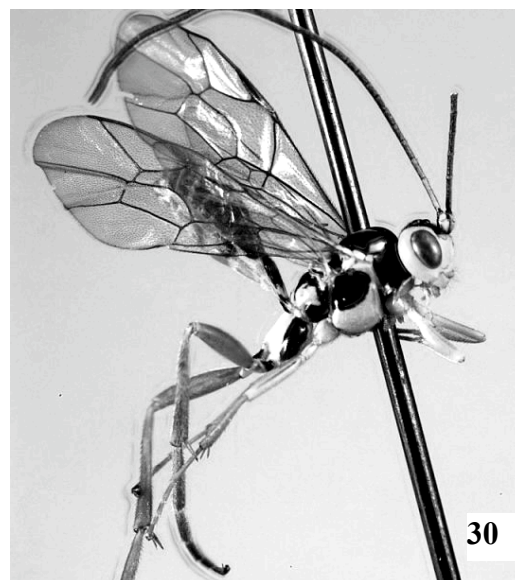
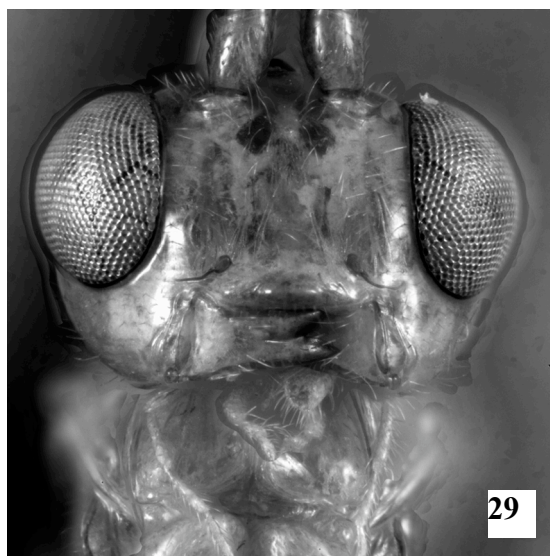




**FIG. 21:** *Physotarsus concavus* sp. nov, habitus, **FIG. 22:** *Physotarsus concavus* sp. nov, face, **FIG. 23:** *Physotarsus concavus* sp. nov., male genitalia, **FIG. 24:** *Physotarsus cordatus* sp. nov., habitus.

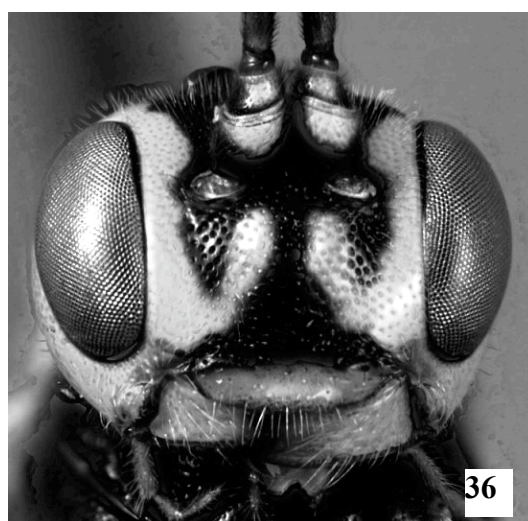
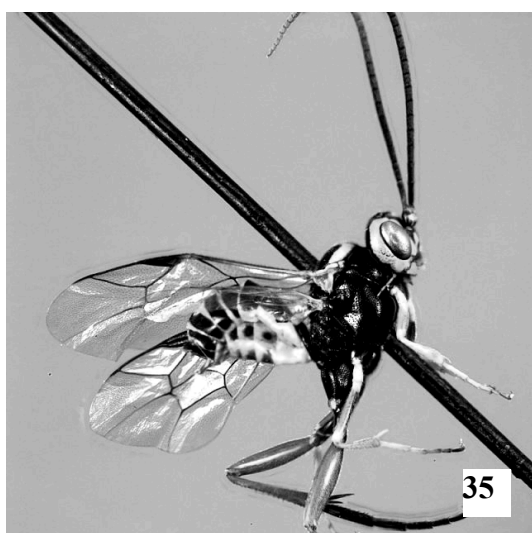
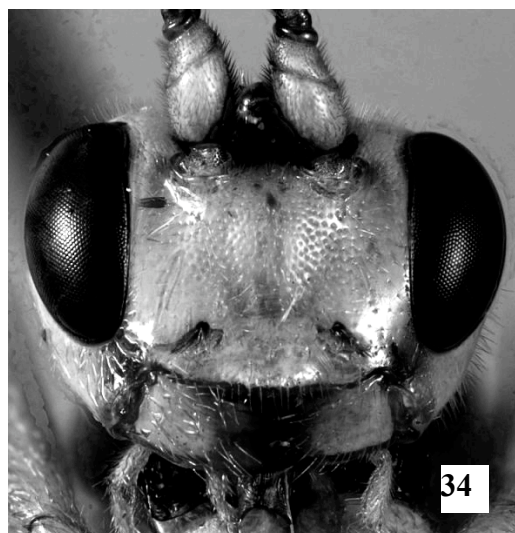
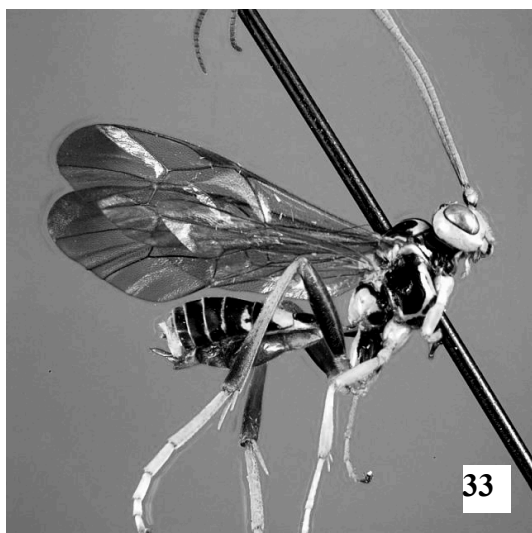


**FIG. 25:** *Physotarsus cordatus* sp. nov., face, **FIG. 26:** *Physotarsus cordatus* sp. nov., male genitalia, **FIG. 27:** *Physotarsus cordatus* sp. nov., scutum (dorsal view), **FIG. 28:** *Physotarsus eliethi* Gauld, 1997, habitus.

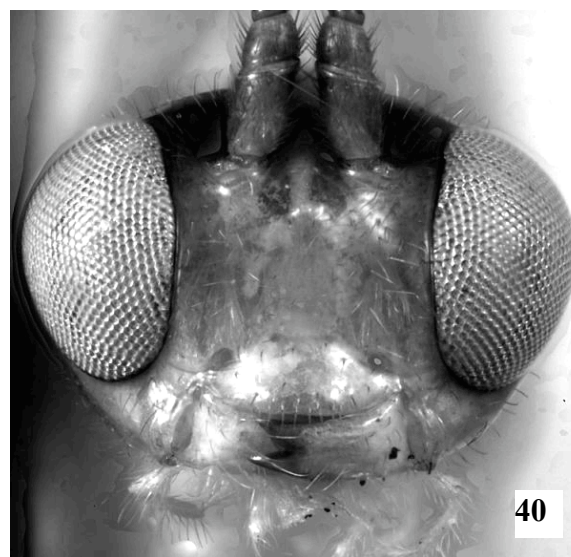
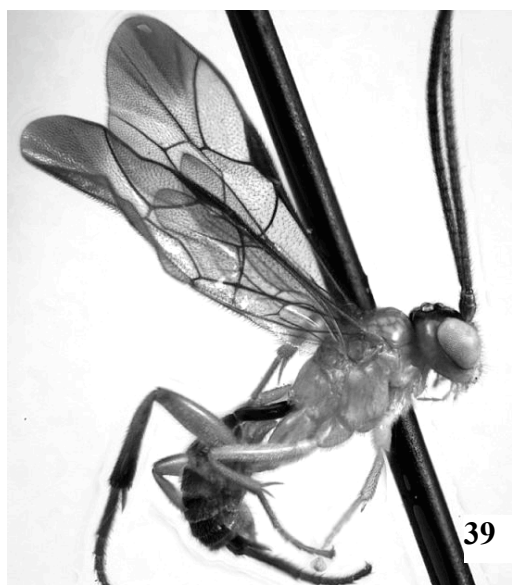
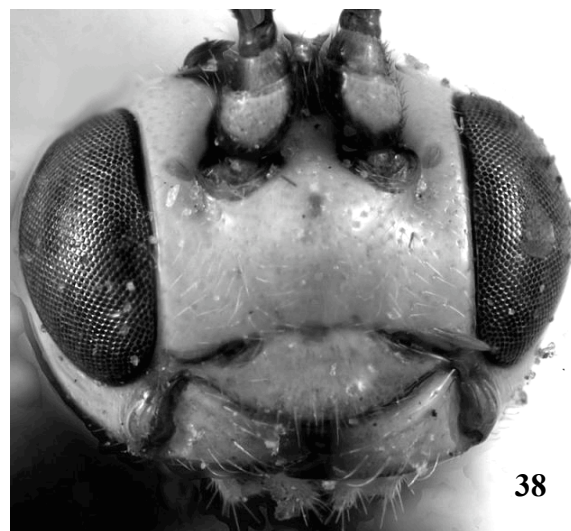
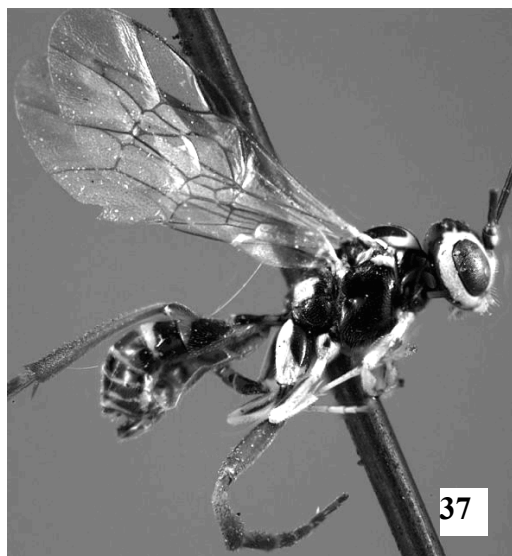


**FIG. 29:** *Physotarsus eliethi* Gauld, 1997, face, **FIG. 30:** *Physotarsus emarginatus* sp. nov., habitus, **FIG. 31:** *Physotarsus emarginatus* sp. nov., face, **FIG. 32:** *Physotarsus emarginatus* sp. nov., male genitalia.



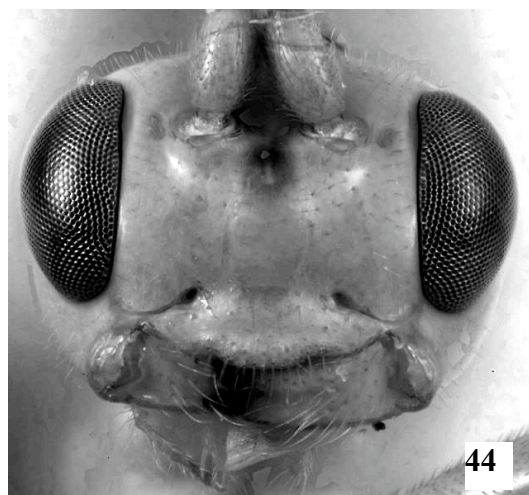
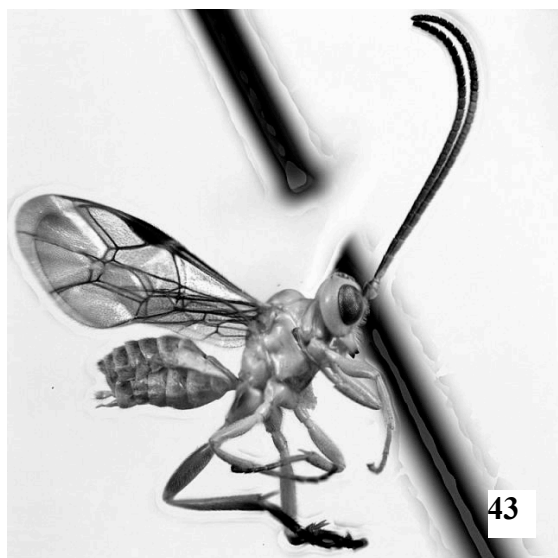
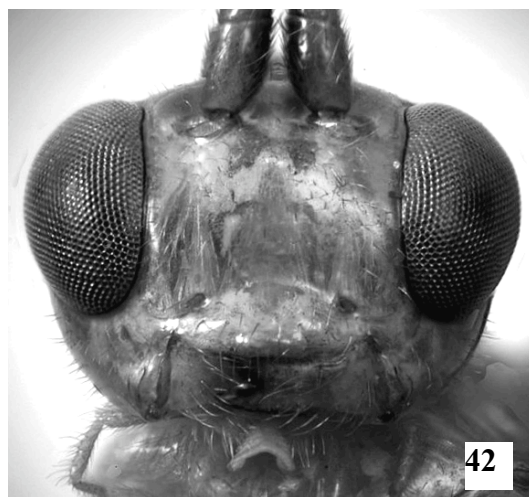


**FIG. 33:** *Physotarsus flavipennis* sp. nov., habitus, **FIG. 34:** *Physotarsus flavipennis* sp. nov., face, **FIG. 35:** *Physotarsus foveatus* sp. nov., habitus, **FIG. 36:** *Physotarsus foveatus* sp. nov., face.

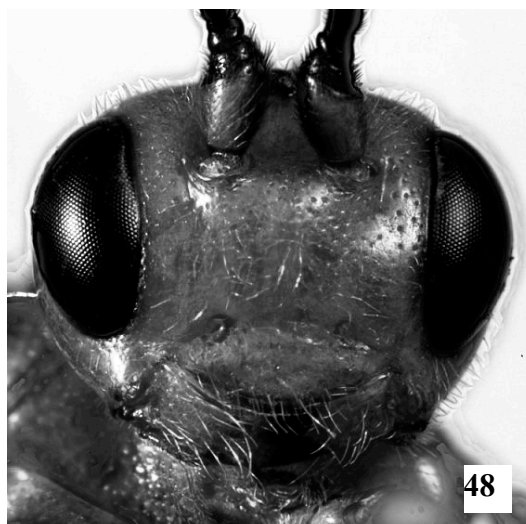


**FIG. 37:** *Physotarsus gineus* sp. nov., habitus, **FIG. 38:** *Physotarsus gineus* sp. nov., face,  
**FIG. 39:** *Physotarsus glabellus* sp. nov., habitus, **FIG. 40:** *Physotarsus glabellus* sp. nov., face.

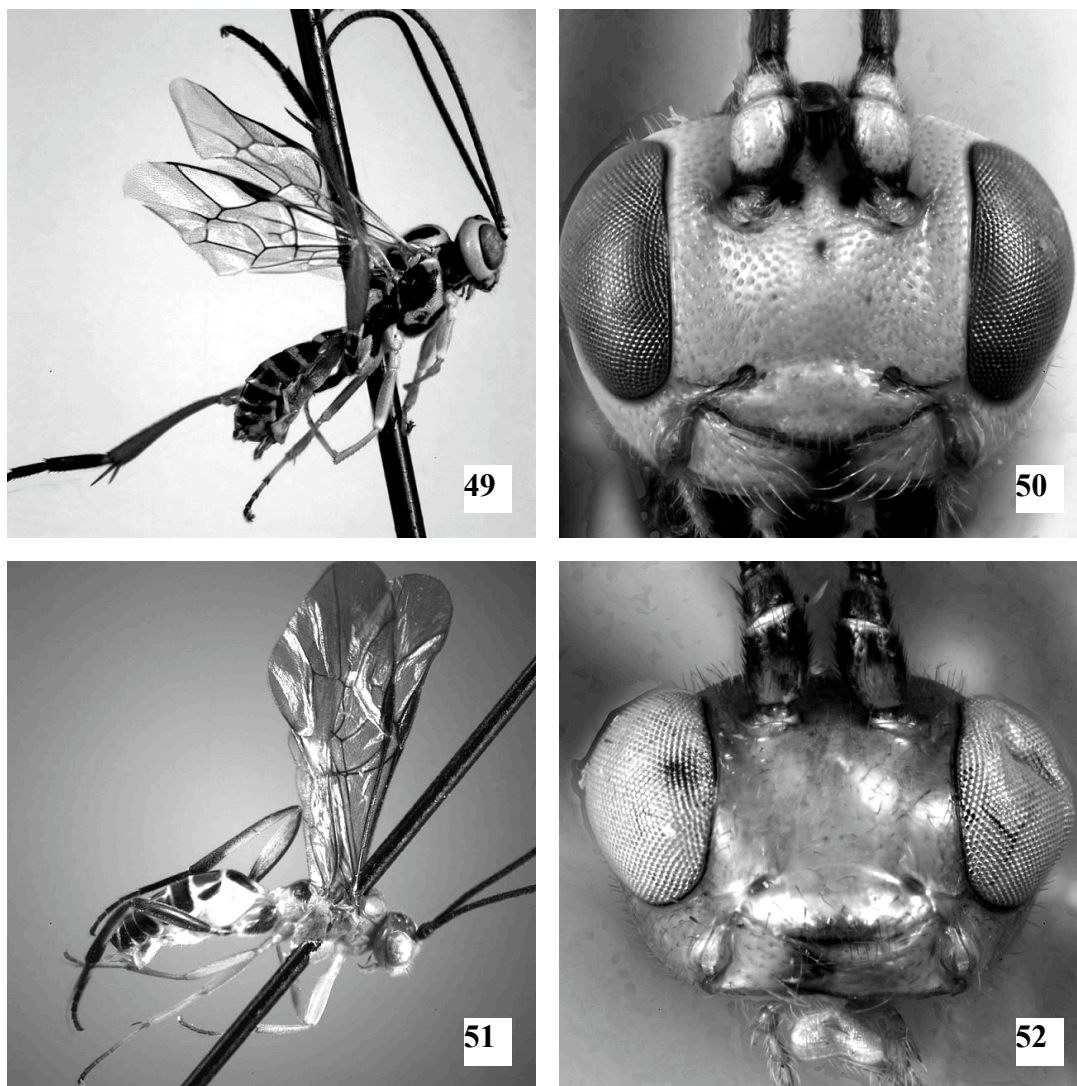




**FIG. 41:** *Physotarsus laucos* sp. nov., habitus, **FIG. 42:** *Physotarsus laucos* sp. nov., face, **FIG. 43:** *Physotarsus luteus* sp. nov., habitus, **FIG. 44:** *Physotarsus luteus* sp. nov., face.

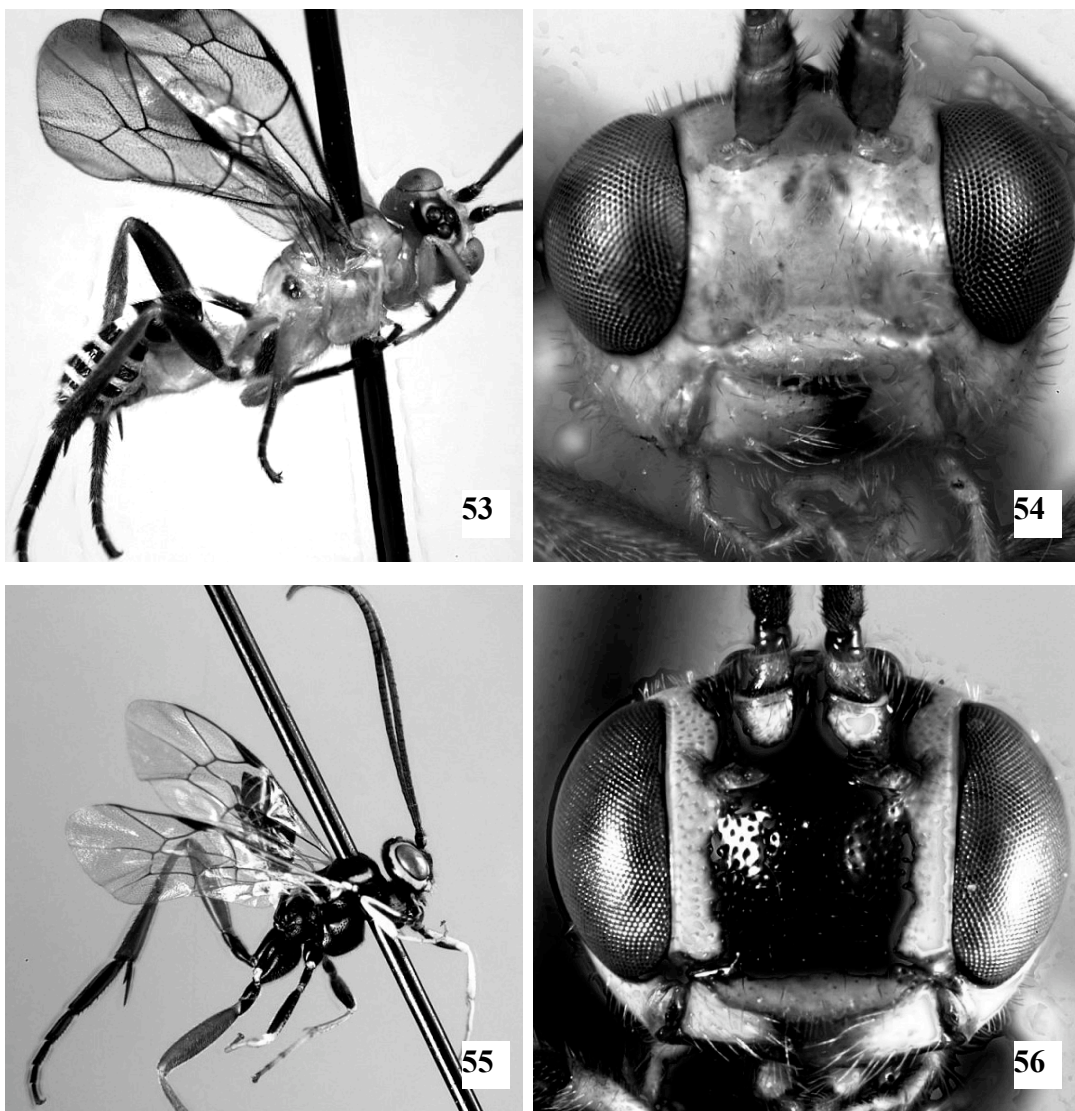


**FIG. 45:** *Physotarsus maculipennis* (Cresson, 1874), habitus, **FIG. 46:** *Physotarsus maculipennis* (Cresson, 1874), face, **FIG. 47:** *Physotarsus melipennis* sp. nov., habitus, **FIG. 48:** *Physotarsus melipennis* sp. nov., face.

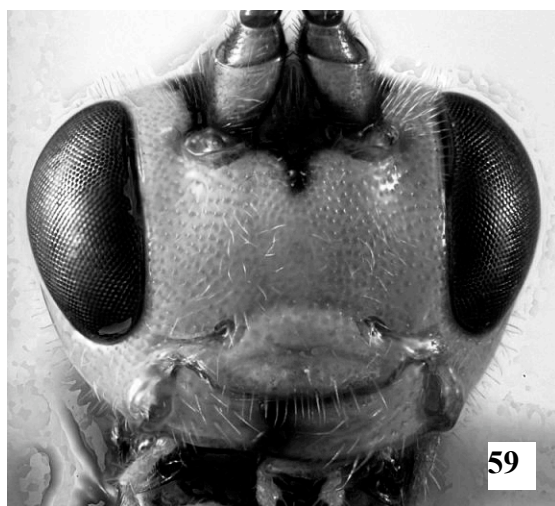
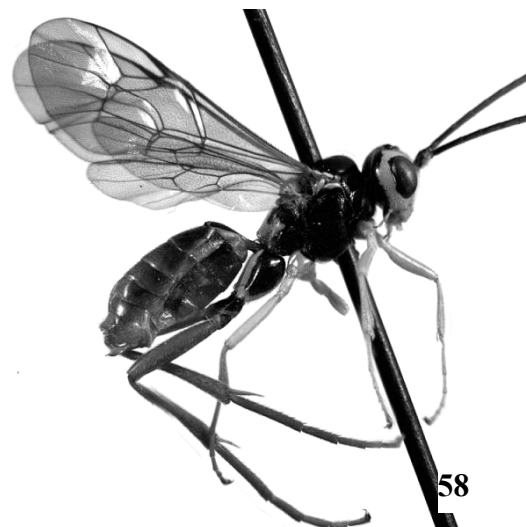


**FIG. 49:** *Physotarsus melotarsus* sp. nov., habitus, **FIG. 50:** *Physotarsus melotarsus* sp. nov., face, **FIG. 51:** *Physotarsus niveus* sp. nov., habitus, **FIG. 52:** *Physotarsus niveus* sp. nov., face.

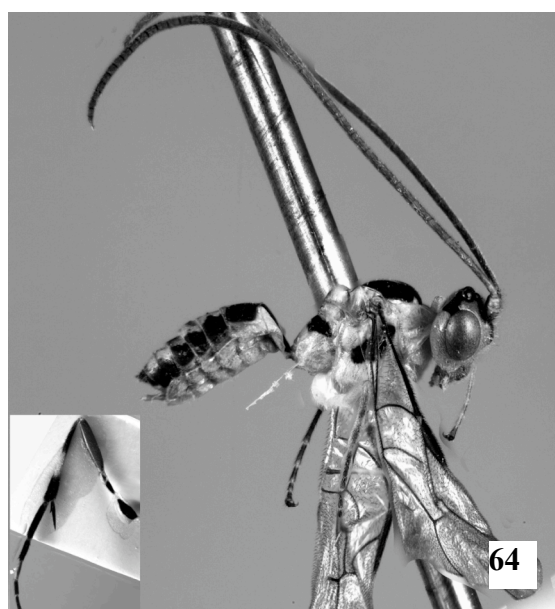
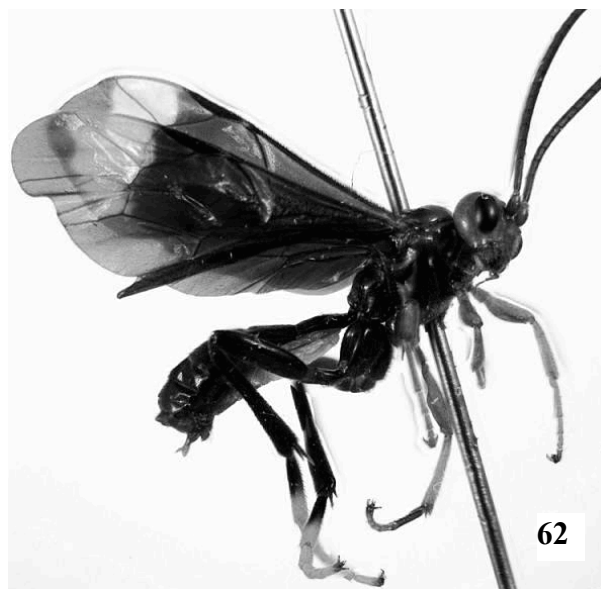




**FIG. 53:** *Physotarsus oculatus* sp. nov., habitus, **FIG. 54:** *Physotarsus oculatus* sp. nov., face, **FIG. 55:** *Physotarsus tonicus* sp. nov., habitus, **FIG. 56:** *Physotarsus tonicus* sp. nov., face ♀.

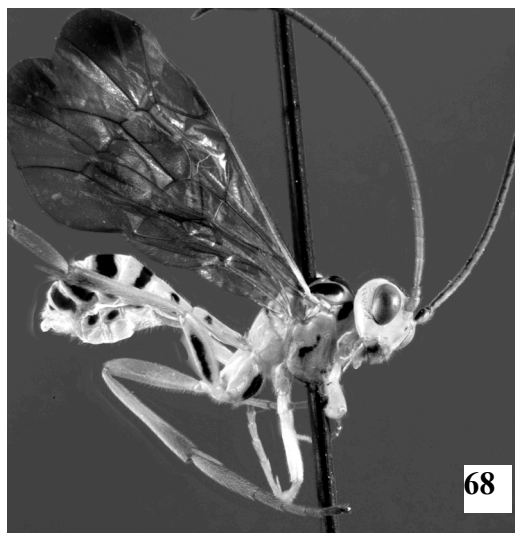
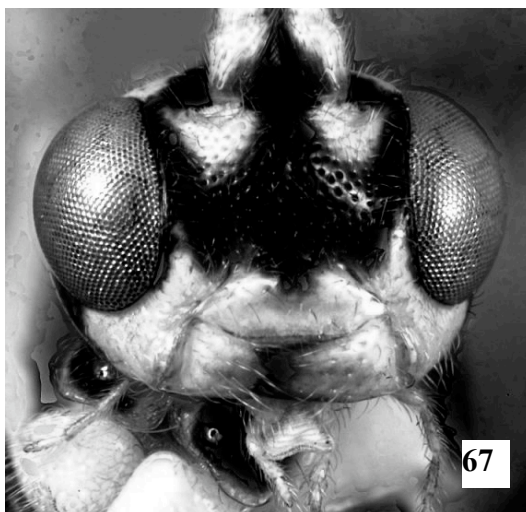
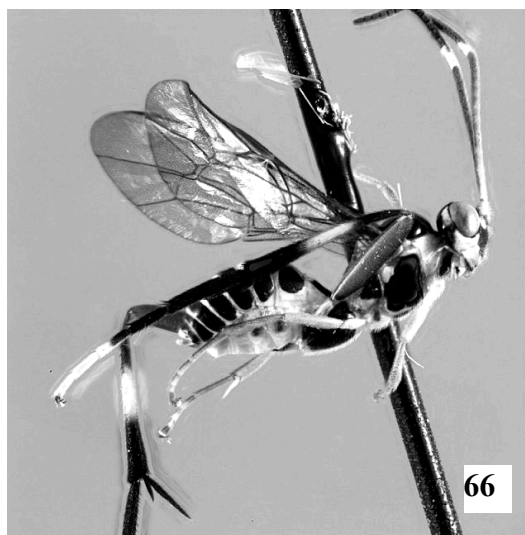
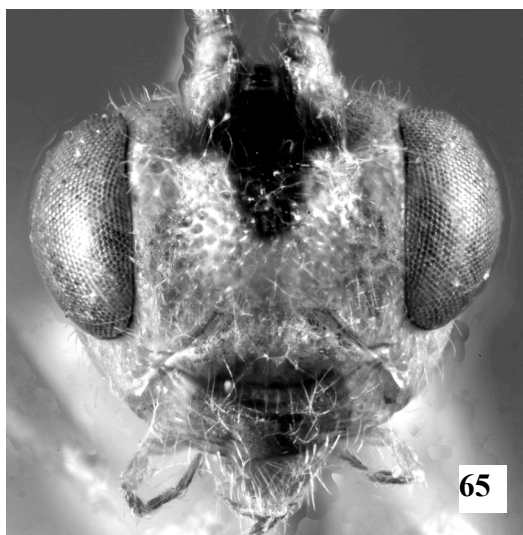


**FIG. 57:** *Physotarsus tonicus* sp. nov., face ♂, **FIG. 58:** *Physotarsus truncatus* sp. nov., habitus, **FIG. 59:** *Physotarsus truncatus* sp. nov., face, **FIG. 60:** *Physotarsus truncatus* sp. nov., male genitalia.

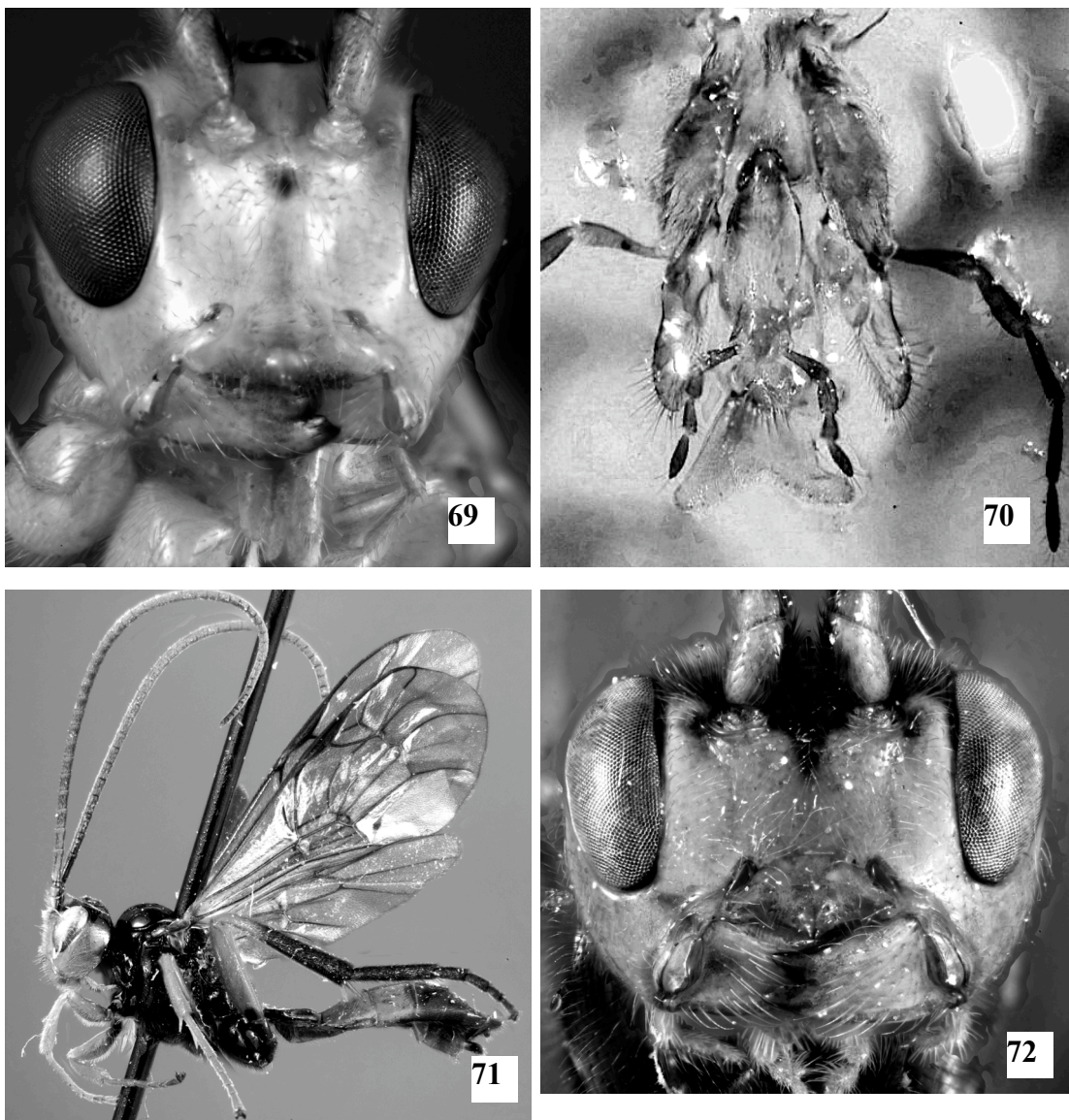


**FIG. 61:** *Physotarsus truncatus* sp. nov., scutum (♀, dorsal view) **FIG. 62:** *Physotarsus varicornis* (Cameron, 1886), habitus, **FIG. 63:** *Physotarsus varicornis* (Cameron, 1886), face, **FIG. 64:** *Catucaba anatterae* Graf, Kumagai, Dutra, 1991, habitus.



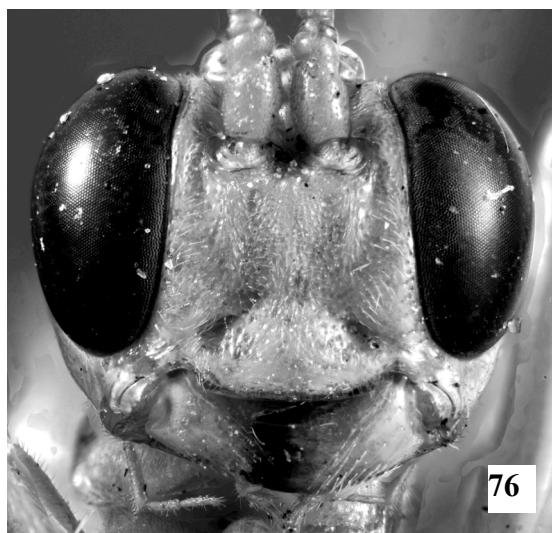
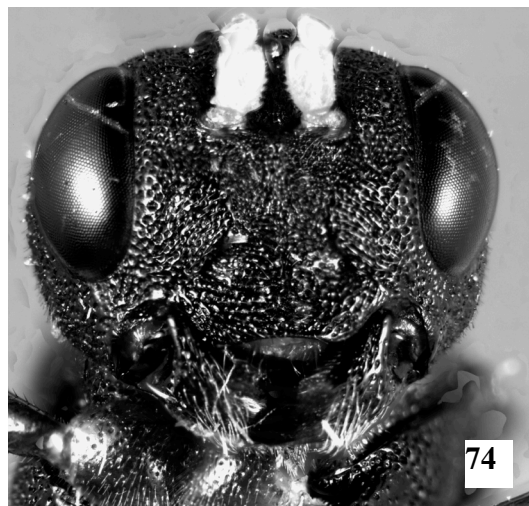
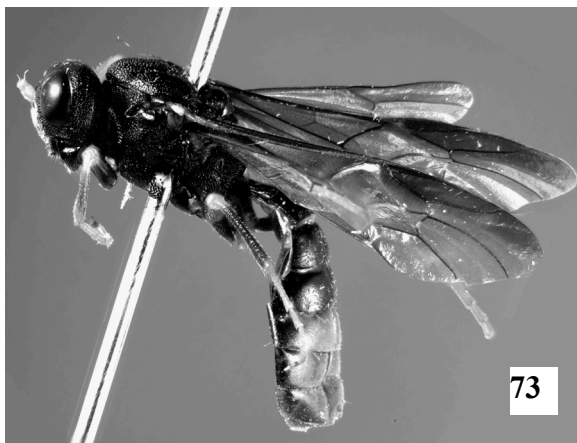


**FIG. 65:** *Catucaba anatterae* Graf, Kumagai, Dutra, 1991, face, **FIG. 66:** *Catucaba montanica* sp. nov., habitus, **FIG. 67:** *Catucaba montanica* sp. nov., face, **FIG. 68:** *Onarion plaumanni* Townes, 1970, habitus.

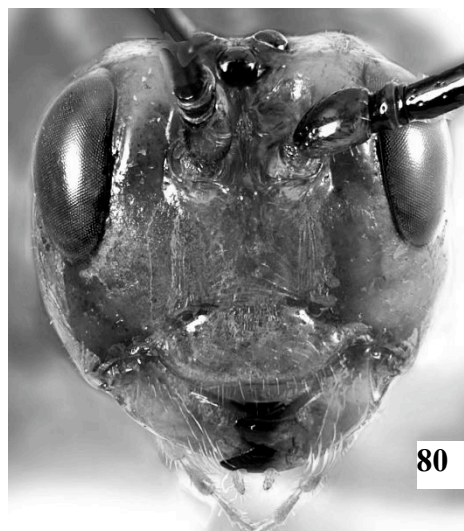
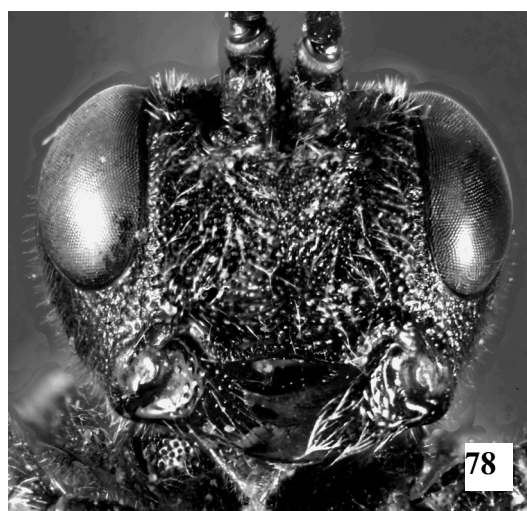


**FIG. 69:** *Onarion plaumanni* Townes, 1970, face, **FIG. 70:** *Onarion plaumanni* Townes, 1970, haustellate mouthparts, **FIG. 71:** *Scolobates auriculatus* Grav. 1829, habitus, **FIG. 72:** *Scolobates auriculatus* Grav. 1829, face.

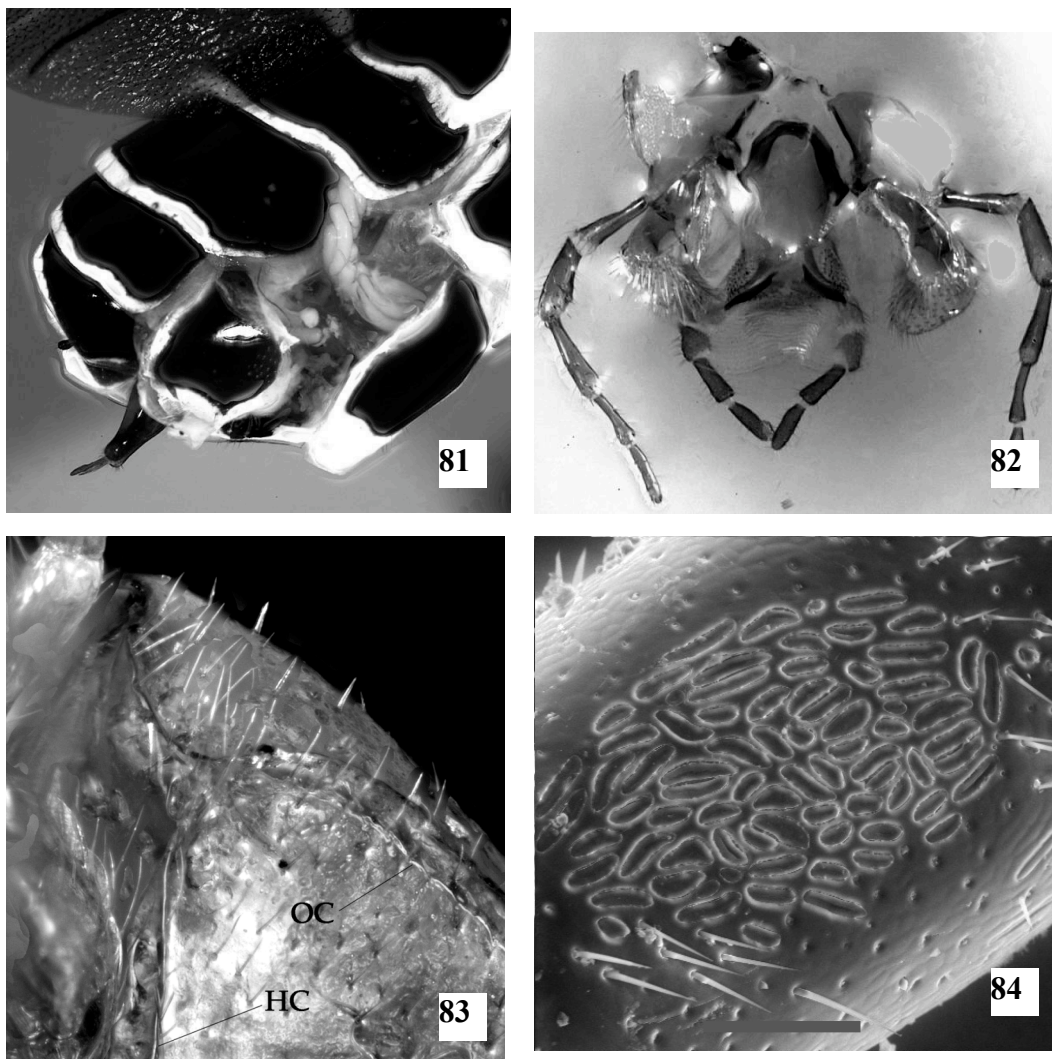




**FIG. 73:** *Dictyopheltes robustus* Gauld, 1984, habitus, **FIG. 74:** *Dictyopheltes robustus* Gauld, 1984, face, **FIG. 75:** *Hypopheltes pergae* Cushman, 1924, habitus, **FIG. 76:** *Hypopheltes pergae* Cushman, 1924, face.

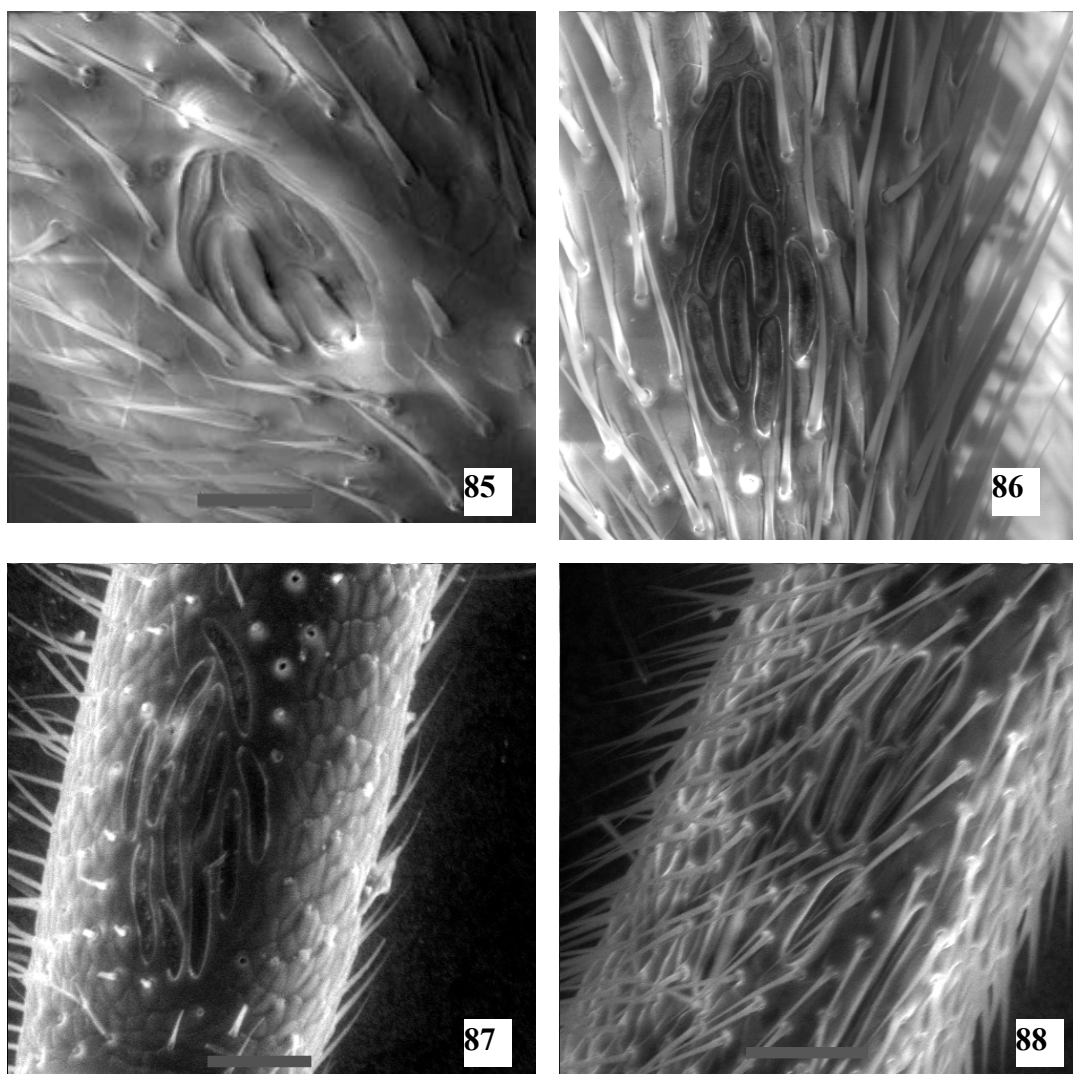


**FIG. 77:** *Pergaphaga nigra* Gauld, 1984, habitus, **FIG. 78:** *Pergaphaga nigra* Gauld, 1984, face, **FIG. 79:** *Westwoodia ruficeps* Brullè, 1846, habitus, **FIG. 80:** *Westwoodia ruficeps* Brullè, 1846, face.

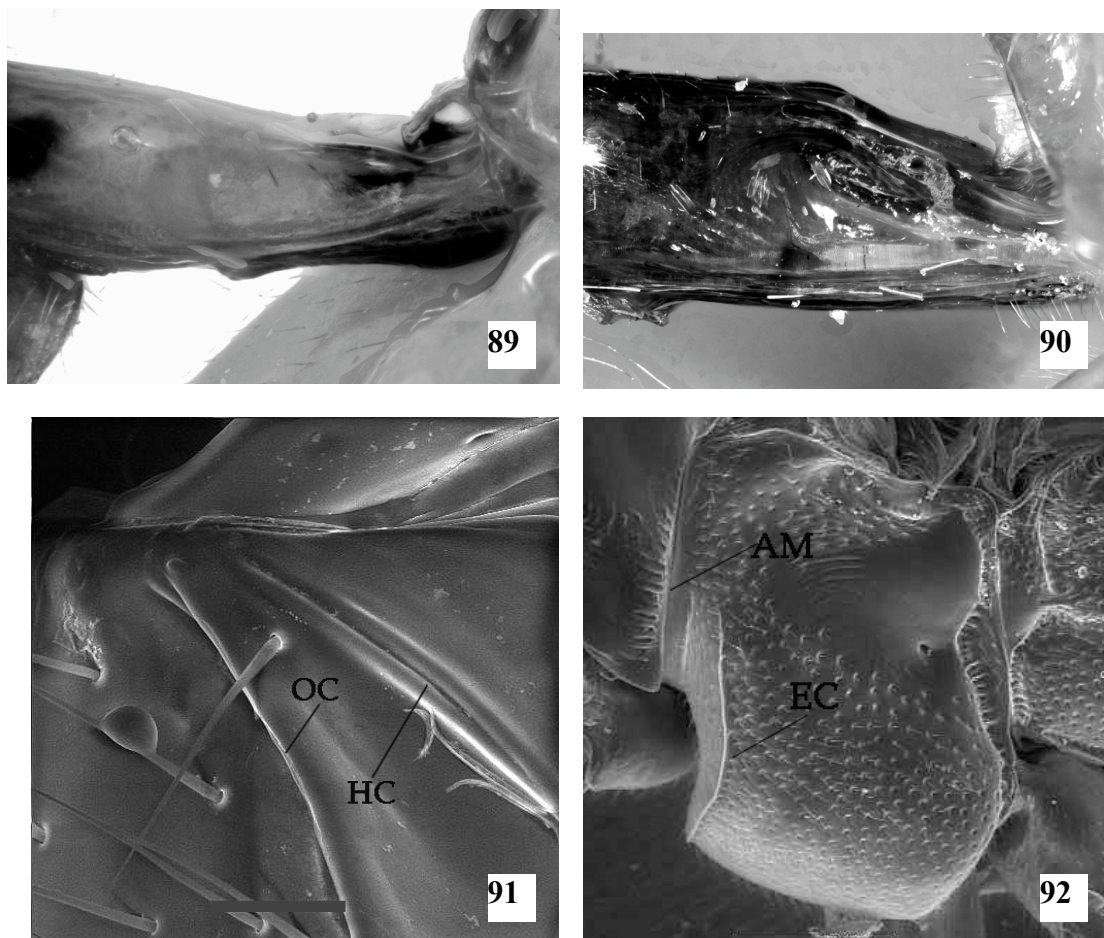


**FIG. 81:** *Westwoodia ruficeps* Brullè, 1846, ♀ abdomen - eggs, **FIG. 82:** *Westwoodia ruficeps* Brullè, 1846, mouthparts, **FIG. 83:** *Westwoodia ruficeps* Brullè, 1846, Head: rear view, OC – occipital carina, HC – hypostomal carina, **FIG. 84:** *Westwoodia ruficeps* Brullè, 1846, tyloid.

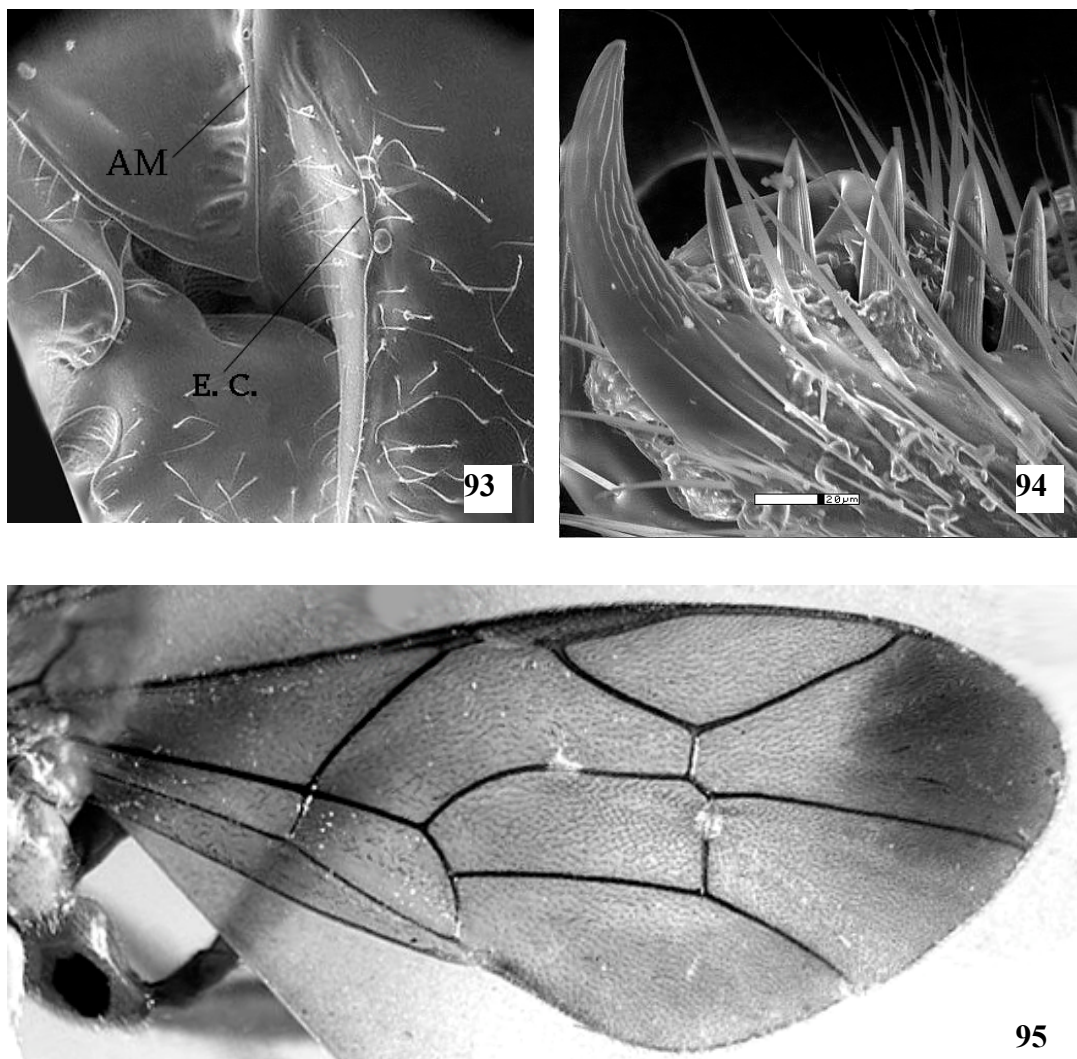




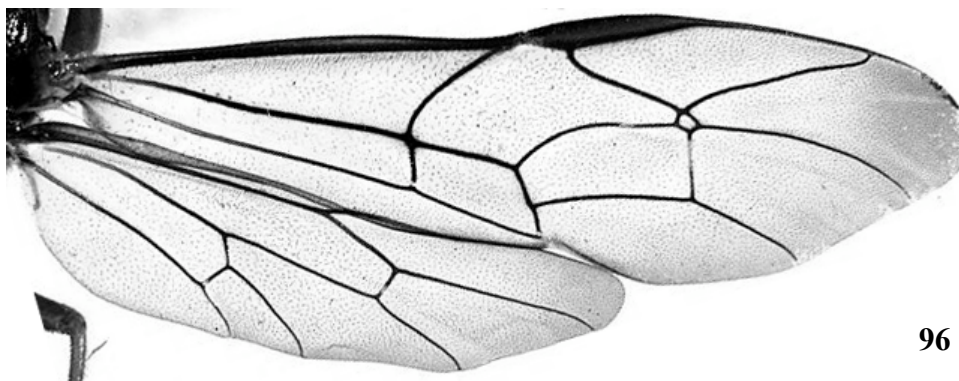
**FIG. 85:** *Physotarsus tonicus* sp. nov., antennal tyloid, **FIG. 86:** *Scolobates auriculatus* Fabricius, 1804, antennal tyloid, **FIG. 87:** *Perilissus townesi* Burks, 1952, antennal tyloid, **FIG. 88:** *Trematopygodes* sp., antennal tyloid.



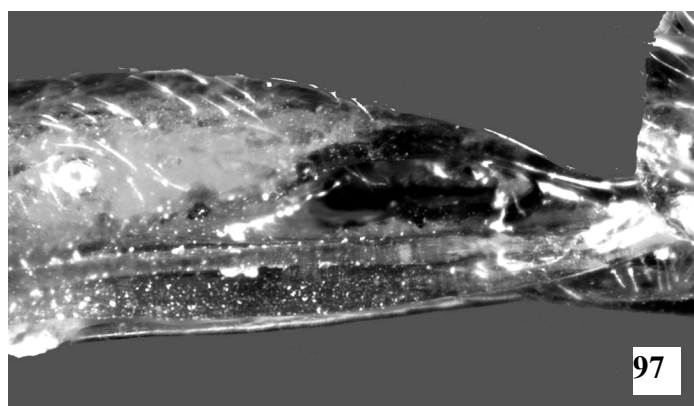
**FIG. 89:** *Onarion plaumanni* Townes, 1970, glymma (group 1), **FIG. 90:** *Hypopheltes pergae* Cushman, 1924, glymma (group 2), **FIG. 91:** *Physotarsus niveus* sp. nov., head: rear view. OC – occipital carina, HC – hypostomal carina, **FIG. 92:** *Physotarsus foveatus* sp. nov., EC – epicnemial carina, AM – anterior margin of the mesopleuron.



**FIG. 93:** *Catucaba montanica* sp. nov., EC – epicnemial carina, AM – anterior margin of the mesopleuron. **FIG. 94:** *Physotarsus maculipennis* (Cresson, 1874), claw, **FIG. 95:** *Onarion plaumanni* Townes, 1970, fore wing.



96



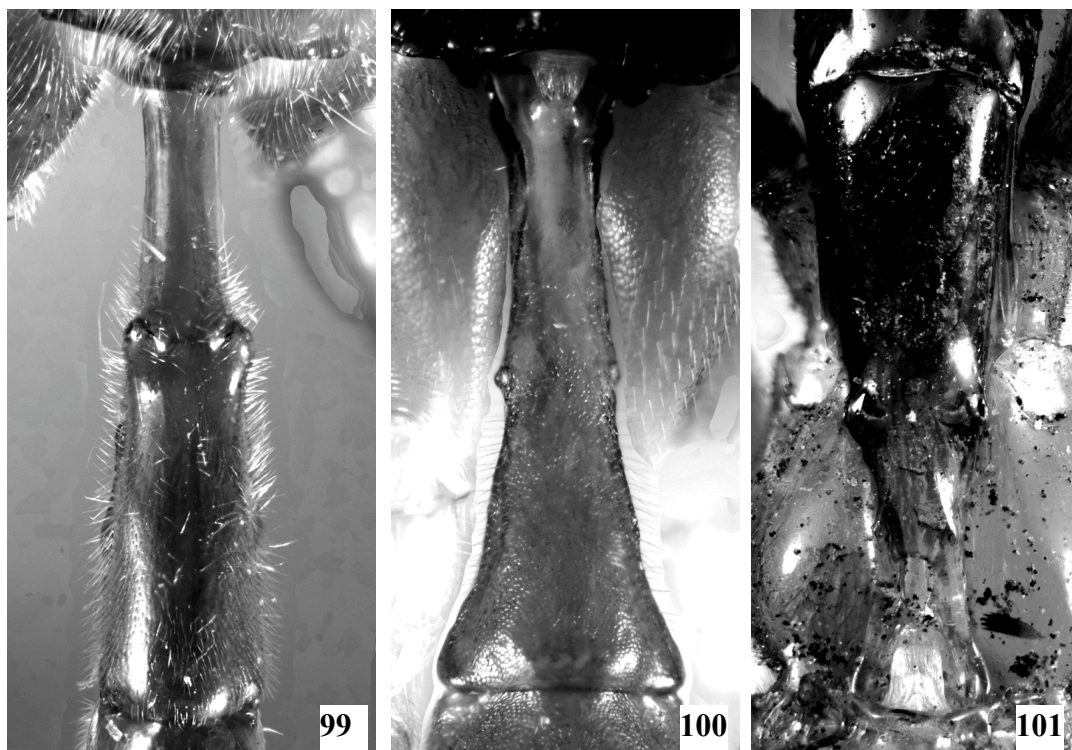
97



98

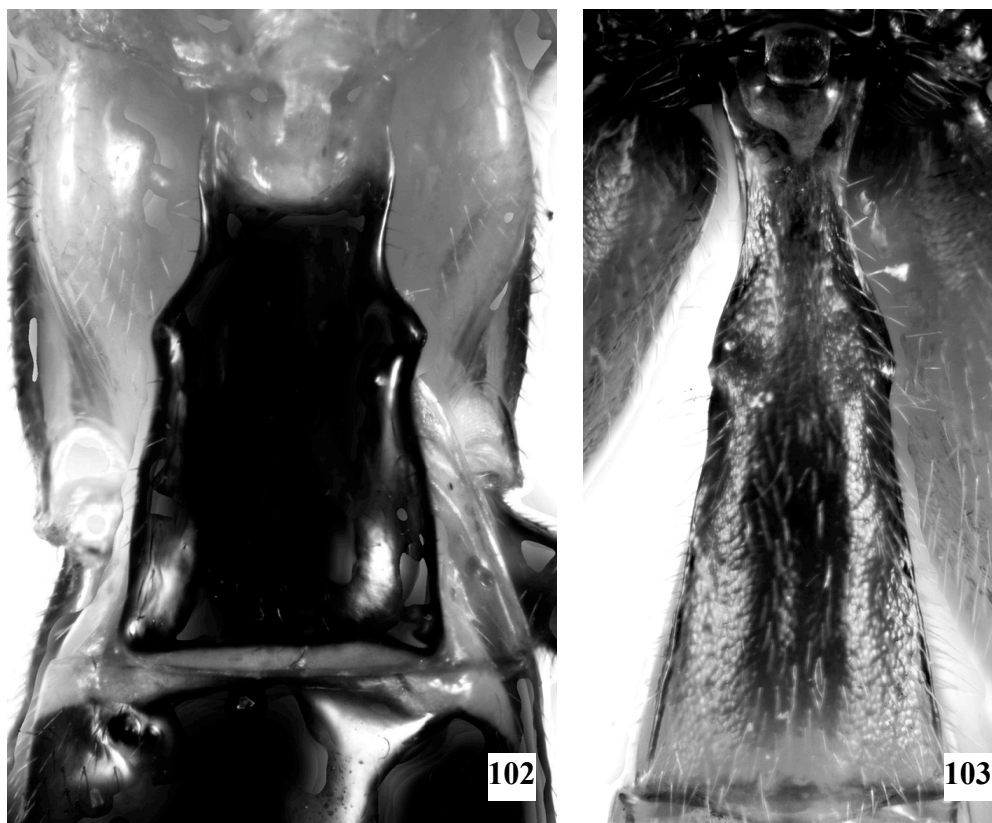
**FIG. 96:** *Hypopheltes* sp. 1, fore and hind wings,  
**FIG. 97:** *Perilissus townesi* Burks, 1952, glymma (group 3),  
**FIG. 98:** *Glypta virginiensis* Cresson, 1870, glymma (group 4)





**FIG. 99:** *Megaceria pagana* Morley, 1913, tergite 1 (dorsal view),  
**FIG. 100:** *Euryproctus* sp. 1, tergite 1 (dorsal view),  
**FIG. 101:** *Hypopheltes pergae* Cushman, 1924, tergite 1 (dorsal view)



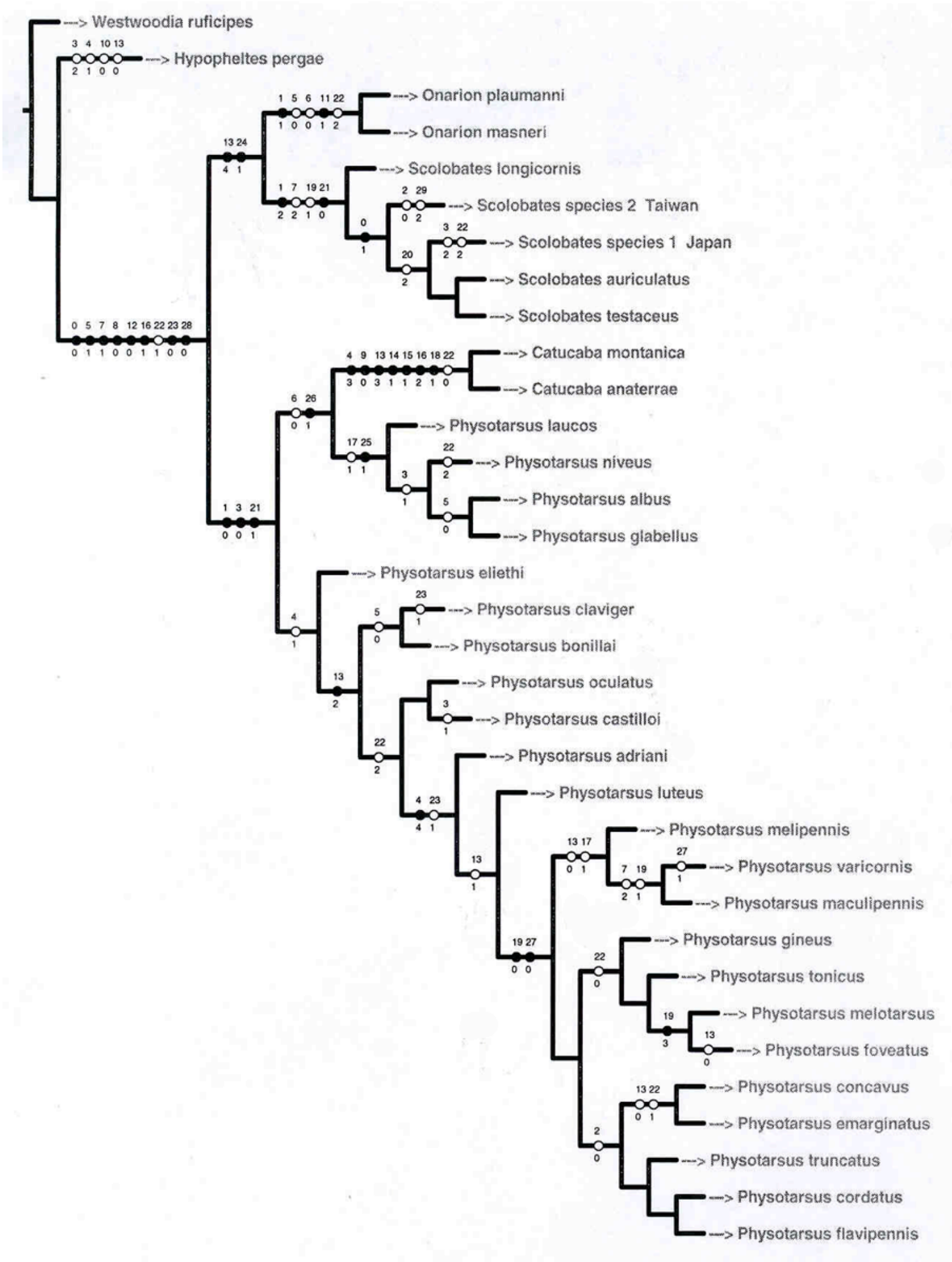


**FIG. 102:** *Physotarsus niveus* sp. nov., tergite 1 (dorsal view),  
**FIG. 103:** *Perilissus townesi* Burks, 1952, tergite 1 (dorsal view).

**TABLE 2: Matrix 1**  
**Phylogenetic analysis of *Physotarsus***

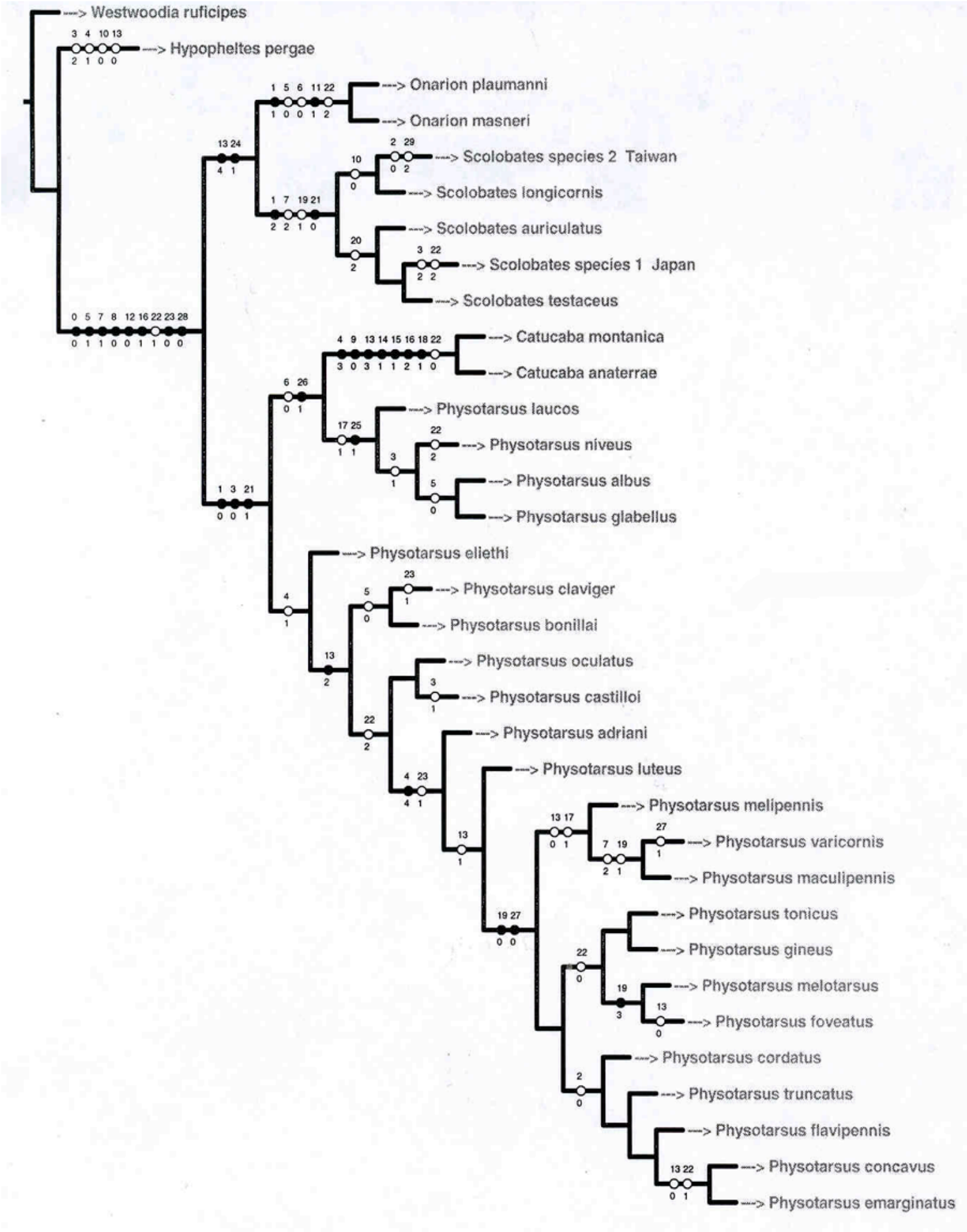
| OTUS                                 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
|--------------------------------------|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Catucaba anaterae</i>             | 0 | 0 | 2 | 0 | 3 | 1 | 0 | 1 | 0 | 0 | 1  | 0  | 0  | 3  | 1  | 1  | 2  | 0  | 1  | 2  | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 0  |
| <i>Catucaba montana</i>              | 0 | 0 | 2 | 0 | 3 | 1 | 0 | 1 | 0 | 0 | 1  | 0  | 0  | 3  | 1  | 1  | 2  | 0  | 1  | 2  | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 0  |
| <i>Hypopheltes pergae</i>            | 2 | 3 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 1 | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 2  | 2  | 3  | 1  | 0  | 0  | 0  | 1  | 1  | 0  |
| <i>Onarion masneri</i>               | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 2  | 2  | 0  | 1  | 0  | 0  | 1  | 0  |
| <i>Onarion plaumanni</i>             | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 2  | 2  | 0  | 1  | 0  | 0  | 1  | 0  |
| <i>Physotarsus adrianni</i>          | 0 | 0 | 2 | 0 | 4 | 1 | 0 | 1 | 0 | 1 | 1  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 1  | 0  |
| <i>Physotarsus albus</i>             | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 2  | 1  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 0  |
| <i>Physotarsus bonillai</i>          | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 2  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>Physotarsus castilloi</i>         | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 2  | 1  | 1  | 2  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>Physotarsus claviger</i>          | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 2  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>Physotarsus concavus</i>          | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus cordatus</i>          | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus eliethi</i>           | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>Physotarsus emarginatus</i>       | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus flavipennis</i>       | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus foveatus</i>          | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 3  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus gineus</i>            | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus glabellus</i>         | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 0  |
| <i>Physotarsus laucos</i>            | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 0  |
| <i>Physotarsus luteus</i>            | 0 | 0 | 2 | 0 | 4 | 1 | 1 | 0 | 1 | 1 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 2  | 1  | 0  | 0  | 1  | 0  | 0  |
| <i>Physotarsus maculipennis</i>      | 0 | 0 | 2 | 0 | 4 | 1 | 1 | 2 | 0 | 1 | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 1  | 0  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 0  | 0  | 1  |
| <i>Physotarsus melipennis</i>        | 0 | 0 | 2 | 0 | 4 | 1 | 1 | 1 | 0 | 1 | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 2  | 1  | 0  | 0  | 0  | 0  | 0  | 2  |
| <i>Physotarsus melotarsus</i>        | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 3  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus niveus</i>            | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 1  | 0  | 0  |
| <i>Physotarsus oculatus</i>          | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 2  | 1  | 1  | 2  | 0  | 0  | 0  | 0  | 1  | 0  |
| <i>Physotarsus tonicus</i>           | 0 | 0 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus truncatus</i>         | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 2  | 1  | 0  | 0  | 0  | 0  | 0  | 0  |
| <i>Physotarsus varicornis</i>        | 0 | 0 | 2 | 0 | 4 | 1 | 1 | 2 | 0 | 1 | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 1  | 0  | 1  |
| <i>Scolobates auriculatus</i>        | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1  | 0  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 2  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 0  |
| <i>Scolobates longicornis</i>        | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0  | 0  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 0  |
| <i>Scolobates testaceus</i>          | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1  | 0  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 2  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 0  |
| <i>Scolobates species 1 (Japan)</i>  | 1 | 2 | 1 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 1  | 0  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 2  | 0  | 2  | 0  | 1  | 0  | 0  | 1  | 0  | 0  |
| <i>Scolobates species 2 (Taiwan)</i> | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0  | 0  | 0  | 4  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 2  |
| <i>Westwoodia rufipes</i>            | 2 | 3 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 2  | 0  | 1  | 0  | 2  | 3  | 1  | 0  | 0  | 0  | 1  | 1  | 0  |

TABLE 3: Tree 1  
Phylogenetic analysis of *Physotarsus*



**Table 3:** The topology (L=88) is the first of the 2 equally parsimonious trees obtained. Black circles represent the diagnostic character states, whereas clear circles are indicative of homoplasy. The number above each circle corresponds to the character number in the text, and the number below each circle is the character state.

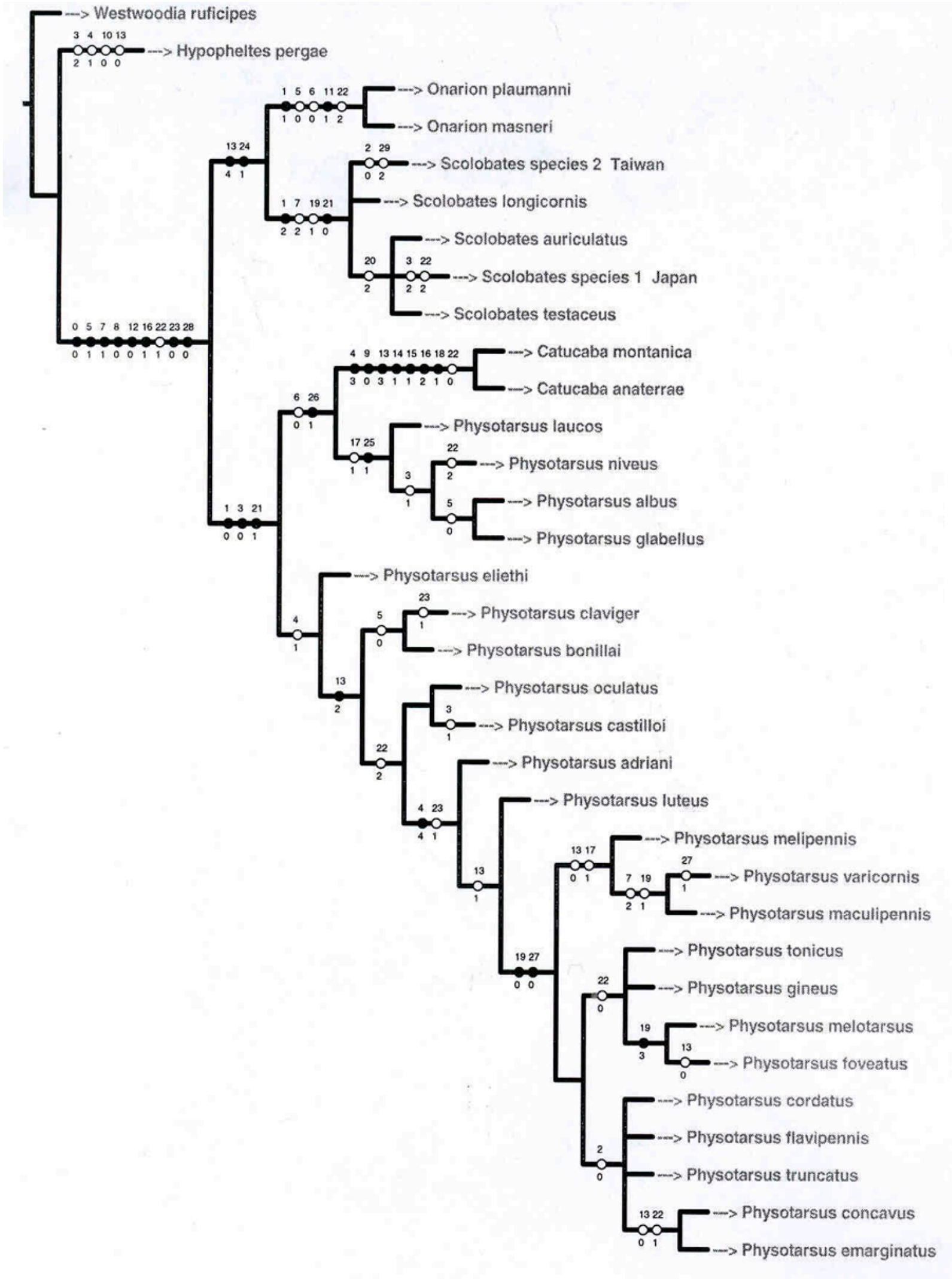
TABLE 4: Tree 2  
Phylogenetic analysis of *Physotarsus*



**Table 4:** The topology (L=88) is the second of the 2 equally parsimonious trees obtained. Black circles represent the diagnostic character states, whereas clear circles are indicative of homoplasy. The number above each circle corresponds to the character number in the text, and the number below each circle is the character state.



TABLE 5: Tree 3  
Phylogenetic analyses of *Physotarsus*: strict consensus tree

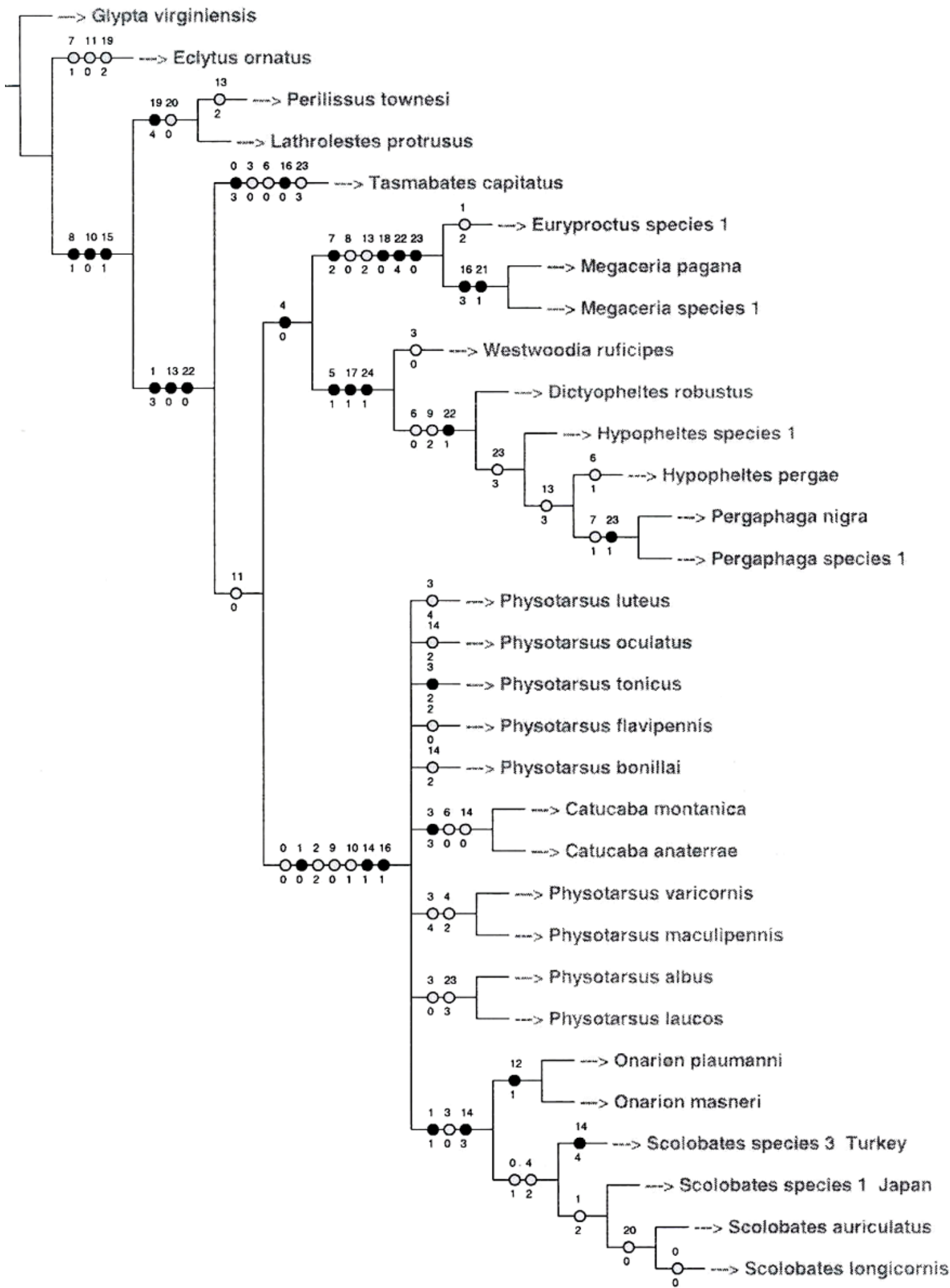


**Table 5:** This tree (L=87) is the consensus topology of trees in Table 1 and 2. Black circles represent the diagnostic character states, whereas clear circles are indicative of homoplasy. The number above each circle corresponds to the character number in the text, and the number below each circle is the character state.

**TABLE 6: Matrix 2**  
**Phylogenetic analysis of Scolobatini**

| OTUs                                 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 |
|--------------------------------------|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Catucaba anaterae</i>             | 0 | 0 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Catucaba montana</i>              | 0 | 0 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Diclyopheltes robustus</i>        | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0  | 0  | 0  | 0  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 2  | 12 |
| <i>Eclytus ornatus</i>               | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1  | 0  | 0  | 3  | 0  | 0  | 2  | 0  | 1  | 2  | 2  | 0  | 2  | 4  | 0  |
| <i>Euryproctus species 1</i>         | 2 | 2 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0  | 0  | 0  | 2  | 0  | 1  | 2  | 0  | 0  | 1  | 1  | 0  | 4  | 0  | 0  |
| <i>Glypta virginiensis</i>           | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1  | 1  | 0  | 3  | 0  | 0  | 2  | 0  | 1  | 3  | 2  | 0  | 3  | 5  | 0  |
| <i>Hypopheltes pergae</i>            | 2 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0  | 0  | 0  | 3  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 3  | 1  |
| <i>Hypopheltes species 1</i>         | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0  | 0  | 0  | 0  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 3  | 1  |
| <i>Lathrolestes protrusus</i>        | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0  | 1  | 0  | 3  | 0  | 1  | 2  | 0  | 1  | 4  | 0  | 0  | 2  | 2  | 0  |
| <i>Megaceria species 1</i>           | 2 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0  | 0  | 0  | 2  | 0  | 1  | 3  | 0  | 0  | 0  | 1  | 1  | 4  | 0  | 0  |
| <i>Megaceria pagana</i>              | 2 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 | 0  | 0  | 0  | 2  | 0  | 1  | 3  | 0  | 0  | 0  | 1  | 1  | 4  | 0  | 0  |
| <i>Onarion masneri</i>               | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 1  | 0  | 3  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Onarion plaumanni</i>             | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 1  | 0  | 3  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Pergaphaga nigra</i>              | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0  | 0  | 0  | 3  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 1  | 1  |
| <i>Pergaphaga species 1</i>          | 2 | 3 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 0  | 0  | 0  | 3  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 1  | 1  | 1  |
| <i>Perilissus townesi</i>            | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0  | 1  | 0  | 2  | 0  | 1  | 2  | 0  | 1  | 4  | 0  | 0  | 2  | 2  | 0  |
| <i>Physotarsus albus</i>             | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 3  | 0  |
| <i>Physotarsus bonillai</i>          | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 2  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus flavipennis</i>       | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus laucos</i>            | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 3  | 0  |
| <i>Physotarsus luteus</i>            | 0 | 0 | 2 | 4 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus maculipennis</i>      | 0 | 0 | 2 | 4 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus oculatus</i>          | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 2  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus tonicus</i>           | 0 | 0 | 2 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Physotarsus varicornis</i>        | 0 | 0 | 2 | 4 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Scolobates auriculatus</i>        | 1 | 2 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 3  | 1  | 1  | 0  | 1  | 3  | 0  | 0  | 0  | 2  | 0  |
| <i>Scolobates longicornis</i>        | 0 | 2 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 3  | 1  | 1  | 0  | 1  | 3  | 0  | 0  | 0  | 2  | 0  |
| <i>Scolobates species 1 (Japan)</i>  | 1 | 2 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 3  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Scolobates species 3 (Turkey)</i> | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1  | 0  | 0  | 0  | 4  | 1  | 1  | 0  | 1  | 3  | 2  | 0  | 0  | 2  | 0  |
| <i>Tasmabates capitatus</i>          | 3 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 3  | 2  | 0  | 0  | 3  | 0  |
| <i>Westwoodia ruficeps</i>           | 2 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0  | 0  | 0  | 0  | 0  | 1  | 2  | 1  | 1  | 2  | 0  | 0  | 0  | 2  | 1  |

TABLE 7:  
Phylogenetic analyses of Scolobatini: consensus topology



**Table 7:** This tree (L=87) is the consensus topology of 101 most parsimonious trees. Black circles represent the diagnostic character states, whereas clear circles are indicative of homoplasy. The number above each circle corresponds to the character number in the text, and the number below each circle is the character state.

**VITA**

*Name:* Kira Zhaurova

*Address:* 119 (C) Biological Control Building  
Texas A&M University  
Department of Entomology  
College Station, TX, 77843

*Education:* A. A., Psychology, Northern Virginia Community College, 2002  
B. A., Biology, George Mason University, 2004